weather & wildlife

volume i:large ungulates

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Montana Fish, Wildlife & Parks

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volume i:large ungulates
an annotated bibliography

Michael R. Frisina
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Habitat Bureau, Wildlife Division

Montana Fish, Wildlife & Parks

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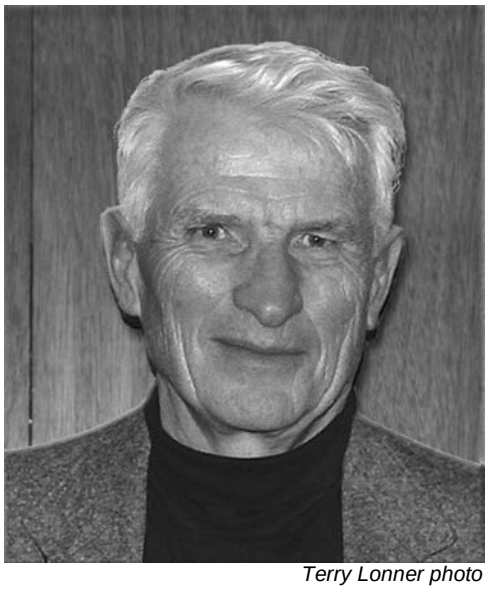
Rough Writers *Studio – Butte, MT*

Harold D. Picton



Terry Lonner photo

Weather & Wildlife Volume I: Large Ungulates
is dedicated to
Dr. Harold D. Picton
Professor Emeritus
Fish and Wildlife Management
Montana State University
in recognition of his extensive research and publication on
the important yet often overlooked relationship between
weather and the lives of wild ungulates.

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Definitions

Climate: the average WEATHER conditions throughout the seasons over a fairly wide or very extensive area of the earth's surface and considered over many years (usually 30 to 35 years) in terms of CLIMATIC ELEMENTS, CLIMATOLOGY, LOCAL CLIMATE, MACROCLIMATE, MESOCLIMATE, MICROCLIMATE, MICROCLIMATOLOGY.

Weather: a general term for the conditions prevailing in the ATMOSPHERE-1, especially in the layer near the ground (TOPOSPHERE), over a short period of time (in contrast to CLIMATE) or at a specific time, at any one place, and as affecting human beings. Temperature, sunshine, pressure and wind, humidity, amount of cloud, precipitation (rain, sleet, hail, snow), the presence of fog or mist are all taken into account.

Clark, Audrey N. 1998. Dictionary of Geography. Penguin Books, New York.

Steve Knapp – Michael R. Frisina photo.

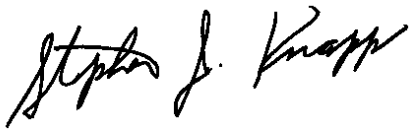
Foreword

In recent years, much ado has been made about climate change, using models that are complex, incomplete and not well understood. Most people, however, readily recognize the effects of daily and seasonal weather on their lives.

So it is also in the lives of wild animals – weather effects their movements, growth and survival. Wildlife management pioneers suggested that the effects of weather should be incorporated into the new science of wildlife studies and management. We have been very slow to do so.

This document is an effort to encourage working field biologists to better understand and incorporate weather and its effects into their wildlife and habitat management recommendations and actions. My hope is this publication will establish weather in its rightful place as a major factor in professional wildlife management decisions as well as

in the public's understanding of weather impacts on wildlife populations.



Steve Knapp
Wildlife Habitat Bureau Chief
October 2008

Michael R. Frisina photo ©2007

Preface

Weather & Wildlife, Volume I: Large Ungulates emphasizes literature describing the influence of weather-related events on large ungulates rather than the larger topic of global climate change. While the bibliography contains a few papers related to modeling, our focus is on the direct and indirect influence of weather events on the life cycle, ecology, and evolution of large wild ungulates.

Although not comprehensive, this bibliography of 395 entries, combined with additional references in the introductory material, provide the wildlife manager, researcher, and student with an extensive cross-section of literature on the subject. Most papers are in English; a few have English abstracts. Research from around the world was sought based upon an extensive data base search including, among others, JSTOR, BioOne, Biological and Agricultural Index,

Wildlife and Ecology Studies World Wide, Zoological Record and Biological Abstracts.

Weather and Wildlife Volume I: Large Ungulates is the first attempt by the Montana Department of Fish, Wildlife & Parks to compile such a reference. We welcome recommendations for inclusion in future editions (*habitat@bresnan.net)*.

R. Margaret Frisina photo ©2004.

Acknowledgements

The authors appreciate the help offered by the staffs of the following libraries in obtaining literature contained in this bibliography:

Renne Library, Montana State University-Bozeman
Mansfield Library, University of Montana-Missoula
Montana State Library-Helena

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Introduction

Weather and the resulting regional climate have long been recognized by wildlife managers as drivers of biotic systems. Early zoogeographers divided the world into regions to explain faunal distribution (Darlington 1957). The faunal regions were, in large measure, driven by climatic differences. Trippensee (1948) recommended that universities developing wildlife management curricula include the study of meteorology and climatology as fundamental sciences. Unfortunately, the recognition of weather's importance has not led to its incorporation into the education of wildlife managers nor the setting of hunting seasons and other management efforts. The need for ecologists to develop an understanding of climatology was reiterated by Stenseth et al. (2003).

Pioneering wildlife scientist Arthur Einarsen (1946) summed up the situation thusly:

"*Although biotic factors, plant successions, complex relationships, and kindred matters enter into ecological interpretations, weather and its cumulative effects rarely receive as much consideration.*

The effects of weather on wildlife are too great to be overlooked or relegated to a place of minor importance."

Since Einarsen made these statements more than 60 years ago, an impressive volume of research has been published verifying his argument that climate and its associated weather events act as drivers in biotic communities. Through evolutionary processes,

impacted extensively by weather, the ungulates we today value look the way they do, live where they do, and often behave as they do. Mackie (1994) described the many physiological and morphological characteristics of mule deer that are adaptations to weather. Similarly Suttie *et al.* (1983) concluded that red deer (*Cervus elaphus*) in Scotland reach a size appropriate to the environment rather than that matching their genetic potential. Generally, weather extremes generate the most attention because they can markedly and suddenly impact wildlife populations in the short term (Dasmann 1964). Weather can also significantly influence predation rates on large ungulates (Allen 1979). We hope this bibliography will encourage wildlife managers to give equal attention to the long-term influences. While weather extremes can play an important role and will always have the potential to wreak havoc with the best laid management plans for a population, weather patterns can impact multiple years. By becoming aware of these patterns, the wildlife manager may have the best hope of taking advantage of good times while being ready to quickly adjust should the pattern change. One point that becomes obvious in these almost 400 bibliographic references is that hunting seasons that "lock in" decisions for multiple years can be counterproductive to the efficient management of wild populations.

By browsing through this bibliography one can see the powerful force weather exerts on wild ungulates. Climate (the average weather conditions for a region over long time spans) influences anatomical features, seasonal distribution, and behavior of wild ungulates. Individual weather events can exert significant influence on the dynamics of individual populations. The survival, body mass and even sex ratio of young-of-the-year has been documented to be profoundly influenced by weather events. Within a climatic region, the vegetation component of habitat is also significantly influenced by weather events, which in turn regulates nutrition, fecundity and productivity, as well as abundance of cover for eluding predators and for thermal regulation (Cain et al. 2008).

For the past few years, the Montana Department of Fish, Wildlife & Parks has discussed the potential for weather to play a greater role in the conservation decision making of the Wildlife Division. The publication of *Weather & Wildlife Volume I: Large Ungulates* is one

step in the direction of recognizing the reality that "…*the effects of weather on wildlife are too great to be overlooked or relegated to a place of minor importance*."

Allen, D. L. 1979. Wolves of Minong: their vial role in wild country. Houghton Mifflin Company, Boston, Massachusetts.

Cain, J. W., B. D. Jansen, R. R. Wilson, and P. R. Krausman. 2008. Potential thermoregulatory advantages of shade use by desert bighorn sheep. Journal of Arid Environments 72:1518-1525.

Darlington, P. J., Jr. 1957. Zoogeography: the geographical distribution of animals. Museum of Comparative Zoology, Harvard, Massachusetts.

Dasmann, R. F. 1964. Wildlife Biology. John Wiley and Sons, Inc., New York, New York.

Einarsen, A. S. 1946. The importance of weather data in wildlife management. Murrelet 27(2):28-33.

Mackie, R. J. 1994. Reacting to weather. Pages 297-300 *in* Deer. D. Gerlach, S. Awater and J. Schnell, eds. Stackpole Books, Mechanicsburg, Pennsylvania.

Stenseth, N. C., G. Otterson, J, W, Hurell, A. Mysterud, M. Lima, K. Chan, N. G. Yoccoz, and B. Ådlandsvik. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. Proceedings Royal Society of London B 270: 2087-2096.

Suttie, J. M., E. D. Goodall, K. Pennie, and R. N. B. Kay. 1983. Winter food restriction and summer compensation in red deer stags (*Cervus elaphus*). British Journal of Nutrition 50:737-747.

Trippensee, R. E. 1948. Wildlife management: upland game and general principles. McGraw-Hill Book Company, Inc., New York, New York.

"Habitat and weather
are keys to game abundance."
Robert Dahlgren
The Pheasant Decline

Bibliography

001

Aanes, R., B-E Sæther, and N. A. Øritsland. 2000. Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. Ecography 23:437-443. Abstract: The relative contribution of density-dependent and density-independent factors on variation in the population growth rate of an introduced population Svalbard reindeer was studied by time series analysis. No significant effects of either direct or delayed density-dependence were found. Annual variation in population growth rate was strongly negatively related to amount of precipitation during winter (i.e. high growth rates occurred when winters were dry). There was no significant relationship between the NAO-index and the population growth rate. However, there was an interaction between population density and the climatic variables, i.e. the effect of climate was stronger at high densities. These results support the view that population fluctuations of arctic ungulates are strongly influenced by stochastic variation in climate. **Key words: reindeer, precipitation, density dependence**

002

Adamczewski, J. Z., C. C. Gates, B. M. Soutar, and R. J. Hudson. 1988. Limting effects of snow on season habitat use and diets of caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada. Canadian Journal of Zoology 66: 1986-1996. Abstract: The insular population of barren-ground caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, is ultimately limited by winter food resources. This study was undertaken to assess forage biomass availability during summer and to determine the effects of snow on forage availability in winter. Vegetation was low in density and diversity, but provided ample forage of high quality in summer for the 2000-2500 caribou existing on the island. Above-ground green biomass averaged only 50-60 $g \cdot m^{-2}$ in mesic and wet meadows, the most productive habitats. Caribou fed almost exclusively in meadows throughout the snow-fee period; willows (*Salix* spp.) constituted 80-90% of rumen contents in caribou collected during the summer. Lichens were scarce and were a major food only at the beginning and end of winter. During mid and late winter, hard-packed snow averaged 4000-9000 $g \cdot cm^{-2}$ in hardness and 50-80 cm in depth on all low-lying vegetation. Under these conditions, caribou cratered only where snow was less than 10-20 cm deep; consequently feeding was limited to the slopes of wind-blown ridges and the tops of high-centre polygons. Forage available under these winter conditions was drastically reduced in quantity and

quality compared with forage available in summer. During winter 1983-1984, snow accumulated rapidly and prolonged deep snow cover was associated with high calf mortality. **Key words: caribou, snow, mortality, nutrition, habitat use**

003

Adams, L. G. 2005. Effects of maternal characteristics and climatic variation on birth masses of Alaskan caribou. Journal of Mammalogy 86(3):506-513. Abstract: Understanding factors that influence birth mass of mammals provides insight to nutritional trade-offs made by females to optimize their reproduction, growth, and survival. I evaluated variation in birth mass of caribou (*Rangifer tarandus*) in central Alaska relative to maternal characteristics (age, body mass, cohort, and nutritional condition as influenced by winter severity) during 11 years with substantial variation in winter snowfall. Snowfall during gestation was the predominant factor explaining variation in birth masses, influencing birth mass inversely and through interactions with maternal age and lactation status. Maternal age effects were noted for females $\leq$5 years old, declining in magnitude with each successive age class. Birth mass as a proportion of autumn maternal mass was inversely related to winter snowfall, even though there was no decrease in masses of adult females in late winter associated with severe winters. I found no evidence of a hypothesized intergenerational effect of lower birth masses for offspring of females born after severe winters. Caribou produce relatively small offspring but provide exceptional lactation support for those that survive. Conservative maternal investment before parturition may represent an optimal reproductive strategy given that caribou experience stochastic variation in winter severity during gestation, uncertainty of environmental conditions surround the birth season, and intense predation on neonates. **Key words: caribou, nutrition, snow**

004

_____. 2003. Marrow fat deposition and skeletal growth in caribou calves. Journal of Wildlife Management 67(1):20-24. Abstract: I evaluated rates of marrow fat deposition and skeletal growth of caribou (*Rangifer tarandus granti*) calves through 20 days of age at Denali National Park, Alaska, USA. Both were negatively correlated with late winter snowfall, indicating the prolonged effects of maternal undernutrition following severe winters. Using regression analyses, I found that the rates of marrow fat deposition and hindfoot growth during the 20 days following birth declined 46% and 68% respectively, over the range of winter severity during this study. These measures of development may indicate a broader array of effects of maternal undernutrition, influencing the vulnerability of caribou calves to predation. **Key words: snow, nutrition, index, predation**

005

_____ and B. W. Dale. 1998. Reproductive performance of female Alaskan caribou. Journal of Wildlife Management 62(4):1184-1195. Abstract: We examined the reproductive performance of female caribou (*Rangifer tarandus granti*) in relation to age, physical condition, and reproductive experience for 9 consecutive years (1987-95) at Denali National Park, Alaska, during a period of wide variation in winter snowfall. Caribou in Denali differed from other cervid populations where reproductive performance

has been investigated, because they occur at low densities (≤0.3/km^2) and experience high losses of young to predation. Females first gave birth at 2-6 years old; 56% of these females were 3 years old. Average annual natality rates increased from 27% for 2-year-olds to 100% for 7-year-olds, remained high for 7-13-year-olds (98%), and then declined for females ≥14 years old. Females ≥2 years old that failed to reproduce were primarily sexually immature (76%). Reproductive pauses of sexually mature females occurred predominantly in young (3-6 yr old) and old (≥14 yr old) females. Natality increased with body mass for 10-month-old females weighed 6 rnonths prior to the autumn breeding season (P = 0.007), and for females >1 year old and weighed during autumn (late Sep - early Nov; P = 0.003). Natality for 2-, 3-, 4-, and 6-year-olds declined with increasing late-winter snowfall (Feb-May; P < 0.039) during the winter prior to breeding. In most years, a high percentage of sexually mature females reproduced, and lactation status at the time of breeding did not influence productivity the following year. However, following particularly high snowfall during February-September 1992, productivity was reduced in 1993 for cows successfully rearing calves to autumn the previous year. High losses of calves to predators in 1992 may have increased productivity in 1993. Losses of young-of-the-year to predation prior to the annual breeding season can be an important influence on subsequent productivity for ungulate populations where productivity varies with lactation status of females at the time of breeding. **Key words: snow, productivity, caribou, nutrition, predation**

006

Albon, S. D. and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65(3):502-513. Abstract: Seasonal changes in crude protein content of graminoids and herbs grazed by red deer were monitored from 1 May, or as soon as snow melt exposed the vegetation, until 15 October at five sites along an altitudinal gradient from coast to inland. Crude protein declined exponentially with time at all sites, but declined most rapidly from initially higher values at inland locations at higher elevations. As a result crude protein was positively correlated with altitude and distance from the coast in early summer and negatively correlated in autumn. The relationships between protein content, date and altitude were used to estimate the quality of the diet of twelve radio-collared female red deer that migrated to summer ranges in the mountains. Individual differences in body weight were significantly related to the estimated, mean crude protein in vegetation available during the summer. Constraints on the timing of migration to exploit the maximal protein concentrations at higher altitudes and the fitness benefits of adaptive ranging behaviour are discussed. **Key words: red deer, migration, nutrition, snow**

007

_____, F. E. Guinness, and T. H. Clutton-Brock. 1983. The influence of climatic variation on the birth weights of red deer (*Cervus elaphus*). Journal of Zoology, Proceedings of the Zoological Society of London 200(2):295-298. Summary: The authors studied the birth weights of red deer over a nine year period (1971-1980) in a single population. Mean calf birth weight showed no correlation with population size. The principal alternative was the effect of climate. There was a close correlation between temperature in April and May and mean birth weight. Their data suggest that for every 1°C increase in mean daily temperature (April and May) birth weight increased by 400g.

The authors suggest several mechanisms: 1) earlier onset of grass growth and an improved nutritional plane of hinds during late gestation, and 2) higher spring temperatures reduce energetic costs of hinds, thus improving nutritional plane. Their data agree with studies in domestic animals that show nutrition in latter pregnancy has the greatest effect on intra-uterine growth and birth weight. **Key words: red deer, bioenergetics, morphology, nutrition, temperature**

008

Anderson, A. E. and E. Medin. 1969. Antler morphometry in a Colorado mule deer population. Journal of Wildlife Management 33(3):520-533. Abstract: Symmetry was demonstrated between left and right antler beam diameters, lengths, and number of points in over 1,200 Cache la Poudre mule deer (*Odocoileus hemionus*) segregated into two age classes. Decreasing annual precipitation, soil moisture, and three- to five-fold decreases in mean yields of two major winter range browse species over a 4-year period did not appear to affect antler development. Simple correlation coefficients (r) of antler beam weight (*Y*) versus antler beam measurements (*X*) of 25 yearling deer were: diameter, 0.62; length, 0.82; and number of points, 0.49. Similar values for 30 deer about 27 months and older were: diameter, 0.82; length, 0.74; and number of points, 0.52. Multiple correlation coefficients derived from antler weight versus these variables were: 0.87 (yearlings) and 0.82 (adults). Antler weight was linearly related to estimated age (0.94), and nonlinearly to eviscerated carcass weight (0.85) in 23 mule deer ranging in age from about 15-77 months. The limitations and possible management applications of these data are described. The antler and environmental data indicate that minimum antler development occurred during 1961 when maximum precipitation and soil moisture prevailed. However, browse yields were not sampled until the fall of 1962, and the 1961 antler development was presumably a response to the winter forage yields of 1960-61, as postulated by Taber (1958). Lacking environmental or deer population data for 1960, causality for the minimum antler development of 1961 is a matter of conjecture. **Key words: mule deer, precipitation, antler**

009

Anthony, R. G. 1976. Influence of drought on diets and numbers of desert deer. Journal of Wildlife Management 40(1):140-144. Abstract: A year-long drought in southeastern Arizona caused an apparent decline in a local mule (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) population. With normal rainfall before the spring of 1970, deer fed primarily on preferred deciduous shrubs such as kidney-wood (*Eysenhardtia polystachya*), fairy-duster (*Calliandra eriophylla*), and range ratany (*Krameria parvifolia*). During the drought period deer utilized evergreen and drought-resistant species. The hot, dry season (April-June) appears to be the most critical period of the year for deer herds in the desert southwest. **Key words: mule deer, drought, diet**

010

Azorit, C., M. Analla, R. Carrasco, and J. Muñoz-Cobo. 2002. Influence of age and environment on antler traits in Spanish red deer (*Cervus elaphus hispanicus*). Zeitschrift für Jagdwissenschaft 48:137-144. Summary: We measured antlers of 484

red deer (*Cervus elaphus hispanicus*) aged between 1.5 and 13.5 years, from Sierra Morena (Southeast Spain) between 1992 and 1998. We determined the effect of year of birth, season of hunting, age group and farm size on the number of tips, the length, the width and the quality of the antlers. The number of harvested animals, an indicator of population density, was included as a covariable. Highest antler quality is obtained in animals at least seven years old. The lowest quality animals were obtained during the hunting season from October 1995 to February 1996, which coincided with the end of an extended period of drought. The best trophies were harvested during the 1996-97 season, the period of highest rainfall during the study. Thus environmental conditions have a major influence on antler size. However, animal density had a strong negative effect on certain types of farms, emphasizing the importance of population management. **Key words: red deer, antler, drought, precipitation**

011

Ball, J., G. Ericsson, and K. Danell. 2001. Among-year variation in moose calf mass related to climate, plant phenology and nitrogen. Oral Session No. 18, Predator-Prey Interactions: Plants and Animals. ESA Annual Meeting. Abstract: We collected 14 years data from northern Sweden (130 000 km^2) to investigate how moose *Alces alces* population dynamics might respond to among-year variations in food caused by weather. We obtained data from a dense network of weather stations, and collected two important foods of different growth forms at these stations every year at the same time. To measure yearly calf growth rate, we collected data on 7688 calves harvested near these weather stations by hunters. Thus, we were able to investigate all three potential links (weather, food and the herbivore's response) at a larger scale than most previous studies. Our analysis revealed large variations (19%) among years in calf mass. This variation was related to weather, plant phenology and nitrogen content in food. Overall, precipitation and temperature during June (the calves' first month of life) explained 35% of the annual variation in calf mass in September; weather during other months was not significant, nor were there significant differences between the stochastic, density-independent factor that affects herbivores by altering feeding conditions. Because calf mass may be correlated with adult size and reproduction, we suggest that a better understanding of ungulate population dynamics may necessitate considering "cohort effects" as a group born in a year with good or bad (June) weather passes through their reproductive years. **Key words: moose, precipitation, temperature**

012

Barichello, N. and J. Carey. 1992. Snow depth as a likely factor contributing to the decline of a sheep population in the central Yukon. Proceedings of the Biennial Symposium, Northern Wild Sheep and Goat Council 8:282. Abstract: A thinhorn sheep population was counted and classified in the Glenlyon Range of the Pelly Mountains in response to a decline in the average age of the sheep kill, and the outfitter's concerns that sheep had severely declined in the area. The population was found to have declined by about 40% of the estimated 1976 population, with the virtual absence of one-half-curl rams and large full-curl rams.

The winter of 1982-83 was a particularly severe one with deeper than average snow conditions during all but one month (p<0.5). The loss of the 1982 cohort and older-aged

animals during this winter, compounded by the reproductive failure of the 1983 lamb crop, adequately explains the decline of the population and the average age of the kill. Relatively poor lamb production in 1981 and 1982 possibly contributed to the decline.

The concentrated distribution of sheep during the winter of 1976-77, in what was possibly an average winter, in comparison to the wide distribution observed in the relatively snow-free winter of 1986-87, further suggests that winter snow conditions may play a key role in the dynamics of sheep in the area. **Key words: wild sheep, snow, distribution, population dynamics, productivity**

013

Barrett, M. W. 1982. Distribution, behavior, and mortality of pronghorns during a severe winter in Alberta. Journal of Wildlife Management 46(4):991-1002. Abstract: Aspects of the distribution, behavior, and mortality of pronghorns (*Antilocapra americana*) were documented in southeastern Alberta during the severe winter of 1977-78. As an apparent response to record snowfall in portions of their range, only 34% of the pronghorns observed during aerial surveys in January and February occupied typical winter ranges characterized by open basins with silver sagebrush (*Artemisia cana*). Many herds selected sites with reduced snow accumulation. Estimated mortality among the approximately 14,360 pronghorns entering the 1977-78 winter was 48.5%. Necropsies revealed significant losses in body weight, kidney fat, and femoral fat content of carcasses when compared with values for animals sampled before winter. Fawns of both sexes and adult males were more susceptible to winterkill than were adult females. Mummification and desiccation were evident in 68 of 82 fetuses examined. Potential adaptive values of the observed behavior and physiological phenomena are discussed. From a management perspective it seems important to recognize that obstacles which restrict the mobility of pronghorns during severe winter conditions can also restrict their ability to survive. **Key words: antelope, snow, habitat use, mortality**

014

Bartmann, R. M. 1986. Growth rates of mule deer fetuses under different winter conditions. Great Basin Naturalist 46(2):245-248. Abstract: Based on forehead-rump length, growth rates of mule deer (*Odocoileus hemionus*) fetuses in Piceance Basin, Colorado, were slower during severe winters than during moderate ones. Growth rates in both situations were slower than reported for both mule deer and white-tailed deer (*Odocoileus virginianus*) fetuses from captive does. **Key words: morphology, mule deer**

015

Beall, R. C. 1974. Winter habitat selection and use by a western Montana elk herd. PhD dissertation, University of Montana, Missoula. A general discussion of winter habitat selection and use by elk. The discussion of movements (radio telemetry) within areas of different snow depth is of some relevance (pp. 62-83). "When the snow depth approached 18 inches [46 cm], elk began moving lower to areas of lesser snow depth. This occurred at shallower snow depths when a heavy crust was present. This does not imply that elk are unable to travel in snow depths greater than 18 inches, for elk were observed to travel through soft snow depths in excess of three feet. However, the energy

expenditure apparently is such, particularly with a crust, that the animals are reluctant to travel through deep snow." (p. 80). (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver, BC, Canada, pp. 15-16.) **Key words: elk, snow, movement**

016

_____. 1973. Winter habitat use in the Sapphire Mountains of western Montana. Pages109-115 *in* E. O. Allen and H. R. Chrest, chairmen. Proceedings of the Biennial Conference of the Western States Elk Workshop, February 20-21, Bozeman, Montana. Summary: Beall notes habitat use in this area is governed by snow conditions. As snow depth increases, elk shift use downslope. Although snow depth affected where elk used the habitat, it did not affect how they used the habitat that seems to be a function of ambient meteorological conditions and solar and thermal radiation. Elk appear to seek the most moderate area under any weather condition. Radiation conditions generated patterns of movement and habitat selection enabling elk to take advantage of radiation and shelter from radiation as weather changed. Unusually warm periods led elk to reduce movement to a minimum to enhance thermoregulation. Elk tended to bed under the most mature trees. As a result of logging in the area, these trees were removed and slash was left within dense stands, hindering travel. Elk sought out non-logged areas. Beall notes this elk avoidance could continue for 20-30 years unless better cleanup is enforced. **Key words: elk, snow, temperature, thermoregulation, behavior, habitat use, movement**

017

Beier, P. and D. R. McCullough. 1990. Factors influencing white-tailed deer activity patterns and habitat use. Wildlife Monographs No. 109. Activity patterns, habitat use, and home range characteristics of white-tailed deer (*Odocoileus virginianus*) on the George Reserve, Michigan, were studied from 1981 to 1984. Deer activity decreased with snow depth, even at slight snow depths, probably because of changes in food availability. Deer activity was maximum at temperatures of 6-16° C and decreased at both higher and lower temperatures. Effects of temperature varied with time of day, season, cloud cover, wind speed, and habitat. Weather variables influenced habitat use during winter, but not during other seasons. Increased use of swamps and decreased use of closed forests, open woodlands and grasslands were associated with increasing snow depth, but could not be explained solely by the swamp microclimate. Swamps also may facilitate deer aggregation to reduce the risk of predation under deep snow conditions. In winter snow depth and to a lesser extent wind speed and temperature had marked effects on habitat use. Increasing snow depth was associated with increased use of swamps and decreased use of other habitats. Deer use of closed forests and marshes was dependent on the combined effects of wind speed and snow depth. Deer use of closed forests increased with wind speed when no snow was on the ground, but deer made little use of forests when snow cover was present regardless of wind speed. Under calm wind conditions, deer increased their use of marshes as snow depth increased, but deer avoided marshes when strong winds were present. Interaction between snow depth and wind speed on deer use of swamps reflected the fact that deer use of swamps increased more when high winds and deep snows co-occurred than would be expected by adding the influence of each factor.

There was an interaction between temperature and cloud cover influencing deer use of grasslands in winter. On cold, winter days (but not warm days), deer increased their use of grasslands as cloud cover decreased, suggesting that deer may move into grasslands to increase their exposure to solar radiation on cold but sunny days. **Key words: white-tailed deer, snow, wind, solar radiation, temperature, habitat use, thermoregulation**

018

Bender, L. C., L. A. Lomas, and J. Browning. 2007. Condition, survival, and cause-specific mortality of adult female mule deer in north-central New Mexico. Journal of Wildlife Management 71(4):1118-1124. Abstract: From December 2001 to December 2004 we monitored 30-44 adult female mule deer (*Odocoileus hemionus*) annually to assess the factors affecting survival and cause-specific mortality. We found adult female survival of 0.63 (SE=0.08), and 0.91 (SE=0.04), 2002-2004, respectively. Starvation was the most common cause of mortality, accounting for 11/23 mortalities. Mean ingesta-free body fat (IFBF) levels of adult females in December were low (6-9%), despite few (0-13%) lactating adult females, indicative of extremely nutritionally deficient summer-autumn ranges throughout the study site. *A priori* levels of IFBF and rump body condition scores (rBCS) were higher in deer than survived the following year regardless of cause of mortality. Logistical analysis indicated that models containing individual body fat, rBCS, mean population body fat, winter precipitation, precipitation during mid- to late gestation, and total annual precipitation were related ($X^2 \geq 9.1$; $P \leq 0.003$) to deer survival, with individual IFBF (β=-0.47)[SE=0.21]; odds ratio = 0.63 [0.42-0.94]) and population mean IFBF (β= -1.94 [SE=0.68]; odds ratio = 0.14[0.04-0.54]) the best predictors; with either variable, probability of dying decreased as fat levels increased. Fawn production was low (2-29 fawns/100 ad F) and, combined with adult survival, resulted in estimated population rates of increase of -35%, -5%, and +6% for 2002-2004, respectively. Deer survival and population performance were limited in north-central New Mexico, USA, due to poor condition of deer, likely a result of limited food resulting from both drought and long-term changes in plant communities. Precipitation during mid- to late gestation was also important for adult female survival in north-central New Mexico. **Key words: precipitation, mule deer, fecundity, mortality, nutrition**

019

_____ and M. E. Weisenberger. 2005. Precipitation, density, and population dynamics of desert bighorn sheep on San Andres National Wildlife Refuge, New Mexico. Wildlife Society Bulletin 33(3):956-964. Abstract: Understanding the determinants of population size and performance for desert bighorn sheep (*Ovis canadensis mexicana*) is critical to develop effective recovery and management strategies. In arid environments, plant communities and consequently herbivore populations are strongly dependent upon precipitation, which is highly variable seasonally and annually. We conducted a retrospective exploratory analysis of desert bighorn sheep population dynamics on San Andres National Wildlife Refuge (SANWR), New Mexico, 1941-1976, by modeling sheep population size as a function of previous population sizes and precipitation. Population size and trend of desert bighorn were best and well described (R^2=0.89) by a model that included only total annual precipitation as a covariate. Models incorporating density-dependence, delayed density-dependence,

and combinations of density and precipitation were less informative than the model containing precipitation alone (ΔAICc=8.5-22.5). Lamb:female ratios were positively related to precipitation (current year: $F_{1,34}$=7.09, *P*=0.012; previous year: $F_{1,33}$=3.37, *P*=0.075) but were unrelated to population size (current year: $F_{1,34}$=0.04, P=0.843; previous year: $F_{1,33}$=0.14, P=0.715).Instantaneous population rate of increase (*r*) was related to population size ($F_{1,33}$=5.55; P=0.025). Precipitation limited populations of desert bighorn sheep on SANWR primarily in a density-independent manner by affecting production or survival of lambs, likely through influences on forage quantity and quality. Habitat evaluations and recovery plans for desert bighorn sheep need to consider fundamental influences on desert bighorn populations such as precipitation and food, rather than focus solely on proximate issues such as security cover, predation, and disease. Moreover, the concept of carrying capacity for desert bighorn sheep may need re-evaluation in respect to highly variable (CV=35.6%) localized precipitation patterns. On SANWR carrying capacity for desert bighorn sheep was zero when total annual precipitation was <28.2 cm. **Key words: wild sheep, precipitation, fecundity, nutrition**

020

Beyers, J. A. and J. T. Hogg. 1995. Environmental effects on prenatal growth rate in pronghorn and bighorn: further evidence for energy constraint on sex-biased maternal expenditure. Behavioral Ecology 6:451-457. Abstract. Byers and Moodie (1990) proposed that high levels of maternal expenditure in polygynous ungulates limit the ability of mothers to support elevated male fetal and neonatal growth rates. This hypothesis assumes that females in high-expenditure species are at or near the maximum level possible and that females in lower-expenditure species are not. To test this assumption, we examined our long-term data on reproduction of pronghorn (*Antilocapra americana*) and bighorn (*Ovis canadensis*) at the National Bison Range (western Montana, USA) and compared gestation lengths, birth weights, and prenatal growth rates of offspring born following summers of low versus average or above average precipitation. In bighorn, these variables were unaffected by the previous summer's rainfall, but in pronghorn, gestation length and prenatal growth rate were significantly lower following dry summers. Extended samples for both species confirmed earlier reports of sex-biased expenditure favoring males in bighorn and the absence of sex-bias in pronghorn. Bighorn prenatal litter growth rates and birth weights, corrected for maternal mass, are 63.5% and 38%, respectively, of pronghorn values. These data support the Byers and Moodie (1990) contention that females of high-expenditure species do not show differential expenditure by offspring sex because they are at a reproductive expenditure maximum, whereas females of lower-expenditure species are able to support excess expenditure in male offspring because optimal allocation to female offspring is farther from such a maximum. **Key words: precipitation, antelope, wild sheep, sex difference, fecundity**

021

Bø, S. and O. Hjeljord. 1991. Do continental moose ranges improve during cloudy summers? Canadian Journal of Zoology 69:1875-1879. Summary: We determined differences in forage quality and observed food and habitat selection by radio-collared moose (*Alces alces*) in southeastern Norway during the summer of 1986 and 1987. June

weather was sunny during 1986 and cloudy and wet during 1987. In the most important browse species (*Betula* sp.), leaf tannin content was lower and the protein:dry matter ratio higher in 1987 than in 1986. Habitat use did not differ significantly between the two summers. During 1987, use of grasses (graminoids) was significantly greater and moose showed a tendency toward greater usage of the most common plant species. The changes in forage quality and choice of plant species by moose during 1987 strengthen earlier assumptions, based on weight comparisons, that continental moose ranges improve during cloudy, wet summers. **Key words: moose, clouds, temperature, precipitation, forage quality, habitat use**

022

Boertje, R. D., P. Valkenburg, and M. E. McNay. 1996. Increases in moose, caribou and wolves following wolf control in Alaska. Journal of Wildlife Management 60(3):474-489. Abstract: Short-term studies in our study area and southeast Yukon have previously documented substantial increases in moose (*Alces alces*) and caribou (*Rangifer tarandus*) following wolf (*Canis lupus*) control. To provide long-term information, we present a 20-year history beginning autumn 1975 when precontrol wolf density was 14 wolves/1,000 km^2. Private harvest and agency control kept the late-winter wolf density 55-80% (mean = 69%) below the precontrol density during each of the next 7 years. Wolf numbers subsequently recovered in $\leq$ 4 years in most of the study area and increased further to between 15 and 16 wolves/1,000 km^2 during a period of deep snowfall winters. The post-hunt moose population increased rapidly from 183 to 481 moose/1,000 km^2 during the 7 years of wolf control (finite rate of increase, λ_r = 1.15) and increased more slowly during the subsequent 12 years (λ_r = 1.05) reaching a density of 1,020 moose/1,000 km^2 by 1994. The Delta caribou herd increased rapidly during wolf control (λ_r = 1.16), more slowly during the subsequent 7 years (λ_r = 1.06), then declined for 4 years (λ_r = 0.78). from a peak density of 890 caribou/1,000 $km^{2.}$ This decline coincided with declines in 2 adjacent, low-density herds (240-370 caribou/1,000 km^2). These caribou declines probably resulted from the synergistic effects of adverse weather and associated increases in wolf numbers. Reduced caribou natality and calf weights were associated with adverse weather. Wolf control was reauthorized to halt the Delta herd's decline in 1993. Similar subarctic, noncoastal systems without effective wolf control have supported densities of 45-417 moose/1,000 km2 (mean = 148, *n* = 20), 100-500 caribou/1,000 km^2, and 2-18 wolves/1,000 km^2 (mean = 9, *n* = 15) in recent decades. In our 20-year history, 7 initial winters of wolf control and 14 initial years of favorable weather apparently resulted in 19 years of growth in moose, 14 years of growth in caribou populations, and a high average autumn wolf density after control ended (12 wolves/1,000 km^2). Benefits to humans included enjoyment of more wolves, moose, and caribou and harvests of several thousand additional moose and caribou than predicted if wolf control had not occurred. We conclude from historical data that controlling wolf populations, in combination with favorable weather, can enhance long-term abundance of wolves and their primary prey, and benefits to humans can be substantial. **Key words: moose, caribou, predation**

023

Bourgarel, M. H. Fritz, J-M Gaillard, M. De Garine-Wichatitsky, and F. Maudet. 2002. Effects of annual rainfall and habitat types on the body mass of impala

(*Aepyceros melampus*) in the Zambezi Valley, Zimbabwe. African Journal of Ecology 40:186-193. Abstract: Body mass is often considered as a good indicator of body condition of individuals in ungulates, hence of their fitness, and thus, may be used as an index to monitor the status of populations subject to harvesting schemes. Here, we report the influence of annual rainfall (a proxy for primary production) and habitat on the body mass of impala in a population cropped for meat in a communal area of Zimbabwe. We analyzed the data from 2 contrasted years for rainfall, in two different habitats. In the good year (i.e. high annual rainfall) impala were heavier than in the poor year, and adult females seemed to be less affected than males by variation in primary production. We show that adult males were suffering from a seasonal decrease in body mass, supposedly linked to the rut, particularly in good habitat. Overall, the habitat effect appeared to be dominated by the rainfall effect, and this may be due to the very high animal densities in the good habitat, i.e. fast resource depletion. Our results also suggest that males (juvenile and adult) are more susceptible to changes in food resource abundance and quality than females, which supports previous studies on sexually dimorphic and polygynous species. **Key words: antelope, precipitation, index**

024

Bowyer, R. T., V. Van Ballenberghe, and J. G. Kie. 1998. Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. Journal of Mammalogy 79(4):1332-1344. Abstract: We studied timing and synchrony of parturition in Alaskan moose (*Alces alces*) in Denali National Park and Preserve, Alaska, from 1990 to 1994. Mean date of birth was 25 May (SD=5.7 days) and did not differ significantly among years. Although moose did not congregate to give birth, parturition was highly synchronized (95% of births occurred in 16 days) with no significant differences among years. Most young moose were killed by predators, especially grizzly bears (*Ursus arctos*), but timing of reproduction had no effect on survivorship of young, which was low (ca. 0.2 by 16 June). We reject the hypothesis that moose timed births to avoid predation. We also measured depth of snow in winter, and precipitation, cloud cover, and temperature in spring; none of these variables was related to timing or synchrony of births. Likewise, quality of willow (*Salix pulchra*) in 3 springs in which percent nitrogen and in vitro dry-matter digestibility of this important forage varied markedly was unrelated to timing of births. We reject the hypothesis that moose timed parturition in response to proximal changes in their environment. We hypothesize that both time and synchrony of parturition in moose are adaptations to long-term patterns of climate that provide the most hospitable conditions to bear and rear young. Consequently, moose may be more susceptible to climatic change than other ungulates that are more adapted to climatic variability. **Key words: moose, parturition**

025

Brandborg, S. M. 1955. Life history and management of the mountain goat in Idaho. Idaho Department of Fish and Game, Boise, Idaho. Notes: In a chapter entitled Natural Hazards, Brandborg states that cold rainy weather may adversely affect survival of kids during the first weeks of their lives, as is the case with domestic goats. One of the most serious consequences of inclement weather is food shortages resulting from heavy snowfalls. Forage conditions on many winter ranges are critical because of excessive snow depths which make much of the forage unavailable. The author further

notes that snow slides are probably responsible for more accidental deaths than any other natural cause. Slide severity depends on snow conditions as a result of varying meteorological conditions. Onset of unusually warm weather can cause loosely packed snow to slide and create serious hazards. During periods of heavy precipitation landslides occur frequently on goat ranges. **Key words: mountain goat, snow, precipitation, nutrition, mortality**

026

Bright, J. L. and J. J. Hervert. 2005. Adult and fawn mortality of Sonoran pronghorn. Wildlife Society Bulletin 33(1):43-50. Abstract: We documented adult mortality and fawn recruitment of Sonoran pronghorn (*Antilocapra americana sonoriensis*) in Arizona. This population is endangered (*N*<30) and is decreasing due to low fawn recruitment and adult mortality. We radiocollared Sonoran pronghorn to monitor survival and recruitment from 1995-2002. We relocated each radiocollared pronghorn during weekly telemetry flights from a fixed-wing airplane and recorded group composition to determine recruitment. Mortalities detected during flights were investigated as soon as possible (i.e., <48 hours) to document adult mortality. Adult mortality rates varied from 11-83%/year. Adult pronghorn were killed by coyotes (*Canis latrans*), bobcats (*Felis rufus*), mountain lions (*Puma concolor*), capturing efforts, drought, and unknown causes. Fawn mortality varied from year to year and was correlated with the amount and timing of rainfall. Drought may be a major factor in the survival of adults and fawns. A lack of nutritious forage and water, caused by dry conditions, led to high fawn mortality and caused adult mortality during a particularly severe drought. Drought also may indirectly affect adult mortality by causing animals to use areas where predators are more successful. Disease may affect mortality but remains largely uninvestigated. Management applications aimed at increasing fawn recruitment and reducing adult mortality should increase the chances of survival of this species. Providing sources of highly nutritious forage during early spring and summer when fawns are susceptible to poor nutrition may increase their chances of survival. Providing water sources and nutritious forage in areas where predators are less successful may increase both adult and fawn survival. Predator control may be useful in limited situations but likely would be prohibitively expensive, with little chance of making a difference over the entire range of Sonoran pronghorn. **Key words: antelope, drought, recruitment, mortality**

027

Brinkman, T. J., C. S. Deperno, J. A. Jenks, B. S. Haroldson, and R. G. Osborn. 2005. Movement of female white-tailed deer: effects of climate and intensive row-crop agriculture. Journal of Wildlife Management 69(3):1099-1111. Abstract: Movements (e.g., migration, dispersal) of white-tailed deer (*Odocoileus virginianus*) vary greatly over the geographic range of the species. Therefore, region-specific, empirical information is needed to effectively manage deer populations. Movements of white-tailed deer have been well documented in forest dominated habitats; however, little information related to white-tailed deer movements exists in intensively (>80%) cultivated areas. From January 2001 to August 2002, we monitored movements of 77 (61 adult, 16 young) female white-tailed deer in southwest Minnesota. We collected 6,867 locations, calculated 130 home ranges, and documented 149 seasonal movements. Fifteen

percent of deer were nonmigratory, whereas 35% were facultative migrators, and 42.5% were obligate migrators. Mean distance between summer and winter home range was 120.1 km. Temperature and snow depth had the greatest influence on initiation of seasonal migration, whereas crop emergence and harvest had minimal effects. Four deer (8%) dispersed a mean distance of 71.3 km with 1 adult female moving a straight-line distance of 205 km. All dispersing deer occupied a temporary staging area for approximately 1 month between previous winter and new summer ranges. Mean home range (95% use area) in winter (5.2 km^2) was over twice as large as home range in summer (2.3 km^2). Movements exhibited by white-tailed deer in southwest Minnesota were influenced by large annual fluctuations in climate and a highly fragmented landscape dominated by row-crop agriculture. We provide data beneficial to biologists managing northern populations of white-tailed deer in fragmented environments by detailing the relationship between climate, intensive agriculture, and deer movements. **Key words: white-tailed deer, migration, snow, temperature**

028

Brown, D. E. 1984. The effects of drought on white-tailed deer recruitment in the arid Southwest. Pages 7-12 *in:* P. R. Krausman and N. S. Smith, editors. Deer in the Southwest: A Workshop. Arizona Cooperative Wildlife Research Unit and University of Arizona, Tucson. Abstract: Seasonal drought controls white-tailed deer distribution in the Southwest and is a major factor determining fawn recruitment rates. Multiple correlation analysis showed a significant relationship between the number of observed fawns per 100 does with preceding June and November drought indices and with the age structure of the population as inferred from hunting success the previous year (R^2 = 0.52; $P \leq$ 0.01). **Key words: white-tailed deer, drought, precipitation, recruitment**

029

_____, D. Warnecke, and T. McKinney. 2006. Effects of midsummer drought on mortality of doe pronghorn (*Antilocapra americana*). Southwestern Naturalist 51(2):220-225. Abstract: We found that the number of doe pronghorn (*Antilocapra americana*) seen on summer surveys in 3 areas in the Southwest was related to midsummer drought indices, and that annual variations in doe mortality might be more important in determining population levels in dry years than fawn recruitment. If carrying capacity is indeed limited by a lack of nutritious forage during dry years, pronghorn managers might want to consider reducing interspecific and intraspecific competition during such periods and forgoing predator control and translocation efforts. **Key words: drought, precipitation, mortality, antelope**

030

Brown, W. K. and J. B. Theberge. 1990. The effects of extreme snowcover on feeding-site selection by woodland caribou. Journal of Wildlife Management 54(1):161-168. Abstract: The depth and hardness of snowcover are important factors affecting caribou (*Rangifer tarandus*) feeding strategies. We investigated the influence of extreme snow conditions on the distribution and use of feeding sites by caribou in the Red Wine Mountains Region, Labrador, during winter (Dec-Apr), 1982-83 and 1983-84.

The tolerance of caribou to snowcover depth and hardness exceeded all previously reported thresholds. Caribou wintered in areas with mean snow depths of 176.7 cm and, to reach forage, they dug through snow with mean depths of ≤ 123.1 cm. Snowcover depths and hardnesses were similar between feeding areas and adjacent areas of similar habitat. Evidence indicated that caribou are capable of visually distinguishing among snow covered terrain features to locate forage on the ground. **Key words: caribou, snow**

031

Bruggeman, J. E. 2006. Spatio-temporal dynamics of the central bison herd in Yellowstone National Park. Thesis, Montana State University, Bozeman. Abstract: The spatio-temporal dynamics of Yellowstone National Park bison (*bison bison*) are complex and affected by multiple abiotic and biotic mechanisms. In the Madison-Firehole area, which provides winter range for the migratory central herd, this suite of effects is particularly intricate owing to geothermally influenced habitats, severe winter climate, and variability in resource distribution. Understanding factors influencing bison spatio-temporal dynamics is of importance to Yellowstone, which is faced with managing a growing bison population that is expanding its range. I gathered data from 1997-2005 using field methods and used statistical modeling and information theoretic techniques to examine spatial and temporal patterns in bison migration, road and off-road travel, and foraging behavior in relation to abiotic and biotic factors. Numbers of bison migrating were related to density and drought severity, while snow, drought, and density affected timing of migration. The probability of bison travel and spatial distribution of travel corridors were affected by topographic and habitat attributes including slope, landscape roughness, habitat, and distances to streams, foraging areas, and forested habitats. Streams were the most influential landscape features affecting travel and results suggest the bison travel network is defined largely by the presence of streams. Probability of travel was higher in regions of variable topography (i.e., canyons). Pronounced travel corridors existed both in close association with roads and distant from any roads, and results indicate roads may facilitate bison travel in areas. Multiple effects influenced temporal bison travel patterns. Road travel was negatively correlated with road grooming and I found no evidence that bison preferentially used groomed roads during winter. Snowpack, density, and springtime melt were correlated with bison road and off-road travel. Bison foraging area residence times were affected by the ratio of local to landscape scale snowpack, previous foraging experiences, and local and landscape scale competition. Bison patch scale foraging behavior was predominantly affected by snowpack, with biomass and competition having minimal influence. My results indicate bison spatio-temporal dynamics are affected by multiple, interacting, scale-dependent mechanisms. Overall, factors influencing resource availability provide the primary impetus for variability in bison distribution, movements, and foraging behavior. **Key words: bison, drought, snow, migration, population dynamics**

032

Bruns, E. H. 1977. Winter behavior of pronghorns in relation to habitat. Journal of Wildlife Management 41(3):560-571. Abstract: The winter behavior of pronghorn antelopes (*Antilocapra americana*) was studied from 6 January to 12 April 1969 in southeastern Alberta and northern Montana. January, climatically an exceptionally

severe month in the study area, saw a pronounced movement of pronghorns southward. The mean herd size was 39.8±11.5 head. Herds did not mix, nor move more than a few km from local sites during February and March; a distinct disbanding process was noted after 25 March. Fences and roads limited day to day movements. Herd composition counts for 6 herds (221 head) indicated a low fawn proportion (41 fawns to 100 does). The male to female fawn ratio of 42 to 100 indicated poor production or survival of male fawns. Pronghorns were adept at pawing away snow cover to reach their food. They spent 6.2 to 11.5 percent of their feeding time pawing. Interactions at feeding craters and bedding sites indicated a social hierarchy with male adults at the top, followed by female adults, and fawns. Pronghorns selected microhabitats with more favorable conditions than the average for the area as a whole, these being: 63 percent lower wind velocities, 24 percent less snow, and 87 percent softer snow. The daytime activity pattern began with a feeding period shortly after sunrise. Resting animals oriented the longitudinal axis of the body so that their anterior portions were downwind when chill factors were extreme; they also curled their heads alongside the body more often at lower chill factors. **Key words: antelope, behavior, thermoregulation, snow, wind**

033

Burles, D., M. Hoefs, and N. Barichello. 1984. The influence of winter severity on Dall sheep productivity in southwestern Yukon: a preliminary assessment. Proceedings of the Biennial Symposium, Northern Wild Sheep and Goat Council 4:67-84. Abstract: Over the past decade 14 Dall sheep populations in southwestern Yukon were periodically assessed through aerial surveys. Lamb production averaged 28.5% (expressed as lambs per 100 nursery sheep), but large variations were documented between years as well as between populations. For variation in productivity among populations, density was found to be a contributing factor (r=-0.621). Both winter temperature as well as snow were found to have an influence on lamb production the following spring. Data from three weather stations in the area showed that temperature was the more consistent variable between stations, giving a correlation coefficient with sheep productivity of r=-0.661. Snow (total precipitation) showed considerable regional variability in this mountainous region, and its correlation with lamb production the following spring was r=-0.4555. Both weather factors were combined into an index of winter severity by expressing their deviation from the long-term mean value as percentage, positive or negative. This index of winter severity was significantly correlated with lamb production the following spring (r=-0.796), and therefore, had a higher predictive value than either temperature or snow conditions alone, if one very deviant year (1983) was excluded. A factor in this deviation may have been the failure of females to recover from the very severe winter of 1981-82. **Key words: wild sheep, snow, index, temperature, productivity, fecundity**

034

Cain, J. W. III, P. R. Krausman, S. S. Rosenstock, and J. C. Turner. 2006. Mechanisms of thermoregulation and water balance in desert ungulates. Wildlife Society Bulletin 34(3):570-581. Desert ungulates must contend with high solar radiation, high ambient temperatures, a lack of water and cover, unpredictable food resources, and the challenges these factors present for thermoregulation and water balance. To deal with the conflicting challenges of maintaining body temperature within

acceptable limits and minimizing water loss, desert ungulates use a variety of physiological, morphological, and behavioral mechanisms. The mechanisms involved in thermoregulation and water balance have been studied in many domestic and wild African and Middle Eastern ungulates; studies involving ungulates inhabiting North American deserts are limited in comparison. Our objectives were to review available scientific literature on thermoregulation, water balance, and the effects of dehydration in desert ungulates. We discuss the physiological, morphological, and behavioral mechanisms used by ungulates to maintain temperature and water balance in arid environments and the implications for research and management of desert ungulates in western North America. **Key words: solar radiation, temperature, thermoregulation, morphology, behavior**

035

Cameron, R. D. and J. M. Ver Hoef. 1994. Predicting parturition rate of caribou from autumn body mass. Journal of Wildlife Management 58(4):674-679. Abstract: Body condition indices are potentially useful as predictors of fecundity in ungulates. We updated a logistic-regression model of the relationship between probability of parturition for adult caribou (*Rangifer tarandus*) and body mass during the previous autumn (model significance, *P*=0.025). We also derived a model for herd parturition rate on the basis of the logistic-regression for individual females and the mean and standard deviation of body mass. Small shifts in mass distribution result in relatively large changes in parturition rate, emphasizing the importance of minor changes in forage quality and availability, and indicating a need for representative masses for a herd when attempting to make predictions. Because of the difficulties in obtaining unbiased samples and the serious errors inherent in not doing so, we recommend estimating parturition rate directly by determining the reproductive status of a sample of radio-collared adult females or through systematic counts of newborn calves, antlers, and udders. **Key words: fecundity, caribou, parturition**

036

Carbyn, L. N. 1983. Wolf predation on elk in Riding Mountain National Park, Manitoba. Journal of Wildlife Management 47(4):963-976. Abstract: Winter food habits of gray wolves (*Canis lupus*) were studied in Riding Mountain National Park in 1978-79 by tracking radio-marked animals and checking kills on the ground. Elk (*Cervus elaphus*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*) were the major prey species. Ungulate densities for the Park were 1.4 elk, 0.94 moose, and 0.34 deer/km^2. Elk outnumbered moose by 2.4:1 in the study area but, as prey, elk outranked moose by 15:1. Elk formed the main food base for the wolf population. In a mild winter with low snowfall, a pack of 3 wolves killed elk and deer but not moose. A pack of 5 wolves showed a strong preference for elk during a year with deep snow. The mid to late winter kill rate, under unusually deep snow conditions, was 1 elk or moose every 2.7 days. The calculated daily food consumption was 0.21 kg of prey/kg of wolf. Killing of prey in excess of needs occurred in late winter as carcass use was incomplete. Kill rate per wolf was 1 elk/14 days. Kill abandonment was not related to prey size, with the time spent at kills varying from 1.4 to 1.5 days for adults and calves, respectively. Mean straight-line distance between kills was 5.1 km. There was no clear pattern of elk distribution within wolf territories and kills were in a random pattern within territories.

Wolves killed a larger proportion of young and old elk when compared to hunter kills adjacent to the Park. Length of discernible chases varied from 20 to 260 m. Predation on elk calves was greater in early to midwinter, whereas predation on cows increased in late winter. Condition of prey, based on femur fat, was good to excellent. **Key words: elk, snow, predation**

037

Carroll, B. K. and D. L. Brown. 1977. Factors affecting neonatal fawn survival in southern-central Texas. Journal of Wildlife Management 41(1):63-69. Abstract: One hundred and twenty white-tailed deer (*Odocoileus virginianus*) fawns were captured in Lavaca and Gonzales counties in 1971 through 1973. The fawns were 1 to 18 days of age and weighed 1.8 to 6.8 kg. They were observed during May and June in Lavaca County and June and July in Gonzales County. The mean home range of Lavaca County fawns was 32.5, 31.7, and 32.9 ha in 1971, 1972 and 1973, respectively. In Gonzales County, the mean home range was 34.3, 37.9, 16.9 ha, respectively. Mortality rates were 25, 50, and 35 percent in Lavaca County, and 90, 35, and 10 percent in Gonzales County in 1971, 1972, and 1973 respectively; combined fawn loss was 47 percent. Predation accounted for 50 percent of mortality. Disease and starvation accounted for 34 percent. Sixteen percent of the deaths were undetermined. Significant correlations were noted between a declining deer population on poor range and fawn survival. Also, areas that were consistently overpopulated but had not suffered extreme droughts experienced moderate levels of fawn mortality each year. **Key words: white-tailed deer, drought, movement, mortality**

038

Cederlund, G. N., H. K. G. Sand, and A. Pehrson. 1991. Body mass dynamics of moose calves in relation to winter severity. Journal of Wildlife Management 55(4):675-681. Abstract: We measured winter and spring loss of body mass among moose (*Alces alces*) calves in a population in southcentral Sweden (Grimsö). The sample consisted of 522 calves of both sexes killed during October-May from 1983 to 1988. Males were consistently heavier than females (P<0.05). Body masses of moose calves were significantly associated with both winter severity (P<0.05) and the date of kill (P<0.001). Mean loss of body mass was highest in hard winters (13% from Nov to Feb-Mar). Conversely, average net gain in body mass from autumn (Nov) to spring (Apr-May) (20%) was highest in mild winters. Snow depth, but not temperature and precipitation, was significantly associated with loss of body masses during winter (P<0.02). During winter, small calves lost not only a larger proportion of their body mass, but also more kilograms than large calves. **Key words: moose, morphology, snow, temperature, precipitation**

039

Chan, K-S, A. Mysterud, N. A. Øritsland, T. Severinsen, and N. Chr. Stenseth. 2005. Continuous and discrete extreme climatic events affecting the dynamics of a high-arctic reindeer population. Oecologia 145:556-563. Abstract: Climate at northern latitudes are currently changing both with regard to the mean and the temporal variability at any given site, increasing the frequency of extreme events such as cold and warm

spells. Here we use a conceptually new modeling approach with two different dynamic terms of the climatic effects on a Svalbard reindeer population (the Brøggerhalvøya population) which underwent an extreme icing event ("locked pastures") with 80% reduction in population size during one winter (1993/94). One term captures the continuous and linear effect depending upon the Artic Oscillation and another the discrete (rare) "event" process. The introduction of an "event" parameter describing the discrete extreme winter resulted in a more parsimonious model. Such an approach may be useful in strongly age-structured ungulate populations, with young and very old individuals being particularly prone to mortality factors during adverse conditions (resulting in a population structure that differs before and after extreme climatic events). A simulation study demonstrates that our approach is able to properly detect the ecological effects of such extreme climate events. **Key words: caribou, population dynamics, ice, model, mortality**

040

Chappel, R. W. and R. J. Hudson. 1978. Winter bioenergetics of Rocky Mountain bighorn sheep. Canadian Journal of Zoology 56:2388-2393. Abstract: Changes in voluntary dry matter intake, body weight, and resting metabolic rates at 10 and -10°C were measured in four adult Rocky Mountain bighorn sheep from October until May. Voluntary intake in mid-February decreased to 0.55 of that in mid-October. Body weights increased until January after which stasis or slight declines occurred. Resting metabolic rate at 10°C fluctuated without a consistent pattern over winter. Resting metabolic rates at -10°C were lowest in February and highest in May. The lower critical temperatures of fed animals in winter pelage were below -20°C. As temperatures were lowered from -20 to -30°C, metabolic rates increased 1.37- to 1.39-fold. Wind speeds from 4 to 8 m/s increased metabolic rates only at temperatures below -20°C. **Key words: wild sheep, wind, temperature, bioenergetics**

041

Cheatum, E. L. 1951. Disease in relation to winter mortality in deer in New York. Journal of Wildlife Management 15(2):216-220. Summary: Results from a study of lungworm, liver fluke and nose bot infestations of white-tailed deer show a positive correlation between incidences and intensity of infestations by these parasites and the death of deer from 'winter-kill'. A pronounced relationship assumed to be of a causative nature was found between infestation by the deer lungworm (*Leptostrongylus alpenae*) and the pneumonias so frequently found in deer dying during severe winters.

Malnutrition of both qualitative and quantitative character is considered the basic factor predisposing to death. The parasite load accompanied by their characteristic lesions and debilitating effects apparently reduces the chance of deer survival in severe winter. Lack of adequate shelter in some localities with consequent chilling was indicated to be of perhaps as much importance in precipitating death as inadequate food. This was found especially in the case of fawns and old animals. **Key words: white-tailed deer, mortality, disease, temperature, wind, nutrition**

042

Chovancova, B. and D. Gomory. 2000. Influence of some climatic factors and predators on the population size of Tatra chamois in the Tatra National Park. Ibex Journal of Mountain Studies 5:173-183. Abstract: Effect of weather conditions during the birth season and predators on the population of Tatra chamois (*Rupicapra rupicapra tatrica*) was investigated using a series of population counts from 1950 until 1996. Weather conditions were characterized by 16 variables derived from the daily temperature, precipitation and wind records of the Slovak Hydrometeorologcal Institute. Among climatic factors, snow conditions proved to affect the population size. No effect of average or extreme temperatures was identified. Stepwise multiple linear regression was used to identify the effects of population density and predators on the abundance of chamois. Both the actual population density and population growth of chamois proved to be affected by the population density in the preceding year, abundance of wolf and wild boar. No effect of the abundance of lynx as a second major predator of chamois was found. **Key words: snow, chamois, population dynamics**

043

Christianson, D. A. and S. Creel. 2007. A review of environmental factors affecting elk winter diets. Journal of Wildlife Management 71(1):164-176. Abstract: Decades of research have produced substantial data on elk (*Cervus elaphus*) diets in winter, when foraging conditions are most likely to affect population dynamics. Using data from 72 studies conducted in western North America between 1938 and 2002, we collated data on elk diets and environmental variables. We used these data to quantify diet selection by elk and to test whether variation in elk diets is associated with habitat type, winter severity, period of winter, human hunting, and study method. Graminoids (grasses and grass-like plants such as sedges) dominated elk diets and consistently occurred at a higher proportion in the diet than in elk foraging habitats, indicating preference. Forbs commonly made up $\leq$5% of the diet, with no evidence for preference; we conclude that forb use is largely incidental to grazing for graminoids. Browse was consumed in proportion to its availability, implying that the amount of browse in the diet was primarily determined by habitat use rather than selection. Comparing the diets of elk and sympatric ruminants, elk consistently selected graminoids more strongly than sympatric ruminants with the exception of bison (*Bison bison*), suggesting that elk are not environmentally forced to adopt the graminoid-biased diet that they normally select. The proportion of open meadows and grasslands on winter ranges are strongly and positively associated with graminoid consumption by elk. The proportion of graminoids in the diet was significantly lower in elk experiencing severe winter conditions or predation risk from human hunting. The period of winter (early, middle, and late) had only small effects on elk diets, as did the method by which the diet was determined. Overall, variation in elk diets is well-explained by a consistent tendency to select graminoids if available, modified by winter habitat type, predation risk and winter severity, which can constrain habitat selection and access to grazing opportunities. To fully understand variation in foraging behavior, biologists should recognize these broad patterns when interpreting resource selection data. Managers should recognize that inconspicuous behavioral responses to environmental stimuli can alter the diet in ways that probably carry nutritional consequences. **Key words: elk, nutrition, habitat use, snow**

044

Clutton-Brock, T. H. 1983. Climatic variation and body weight of red deer. Journal of Wildlife Management 47(4):1197-1201. Findings: Variation in the fall weights of stags was significantly correlated with mean daily temperatures during the previous December, January and February. The correlation between stag weights and the average mean daily temperature across these 3 months was even higher and this measure of winter temperature accounted for 64% of the variance in stag weights (Fig. 2). The costs of thermoregulation in winter are known to be high in the open habitat of the Scottish highlands (Staines 1977, Grace and Easterbee 1979) and the importance of winter temperatures to stags is supported by evidence that, across Scotland, stag weights increase with mean January temperature and decrease with the mean number of days of snow cover (Watts 1980). In addition, a previous study has shown that antler shedding is delayed after cold winters (Watson 1971). Like stag weight, hind weight was not associated with variation in summer rainfall despite the fact that summer rainfall declined significantly during the 20-year study. Hind weight was not correlated with mean daily temperature in early or late summer. However, unlike stag weight, hind weight was not associated with mean daily temperature between December and February the previous year. Thus our analysis suggests that stag weight, in contrast to hind weight, is strongly influenced by the previous winter conditions. This sex difference may occur because stags enter the winter in poor condition after losing up to 25% of their weight in the October rut, whereas nonlactating hinds enter the winter at maximum weights and in peak condition (Mitchell et al. 1976). In these circumstances, stags may be more vulnerable to exposure than hinds. This may also explain the observed sex differences in use of natural shelter (Jackes 1973, Clutton-Brock et al. 1982a). **Key words: red deer, temperature, thermoregulation, precipitation, behavior**

045

_____ and S. D. Albon. 1989. Red deer in the Highlands. BSP Professional Books, Oxford, United Kingdom. Notes: Chapter 6 is devoted to the topic of weather and red deer populations and its impact on body weight, fecundity, calving date, birth weight, summer calf mortality, winter juvenile mortality, adult mortality and variation in reproductive performance between cohorts. Variation in temperature, snow cover, wind speed and rainfall affect deer populations in three main ways: (1) by raising energy demands for maintenance activities, (2) accessibility of food supplies, and (3) affect on quantity or quality of food resources. **Key words: red deer, snow, temperature, precipitation, wind, mortality, fecundity, nutrition**

046

_____ and _____. 1982. Winter mortality in red deer (*Cervus elaphus*). Journal of Zoology London 198:515-519. Abstract: Previous analysis has suggested that inter-year variation in mortality of adult red deer in Scotland is principally affected by summer weather conditions. Data collected over fourteen years on the Isle of Rhum (Inner Hebrides) show that mortality was negatively correlated with winter temperatures and positively with rainfall in late winter. In conjunction, these two factors accounted for 82% of the observed variation between years. **Key words: red deer, mortality, precipitation, temperature**

047

Cole, E. K. and P. E. Farnes. 2007. Estimating forage production and winter severity on the National Elk Refuge, Jackson, Wyoming. Proceedings of the Western Snow Conference 75:137-140. Abstract: Each October through November, elk and bison migrate to the National Elk Refuge (NER) near Jackson, Wyoming to feed on native forage produced on the Refuge. Usually by late January, standing forage has been utilized or becomes unavailable because of snow and ice, and NER staff then supplies supplemental feed in the form of alfalfa pellets. Supplemental feeding typically ends in early April, when elk and bison migrate back to summer ranges.

For the past 34 years, NER staff has estimated total annual forage produced on the Refuge by clipping vegetation within different plant community types. Average forage production in each plant community type is then accumulated by the number of acres represented by each type to obtain total forage produced on the Refuge.

Keetch Byram Drought Index (KBDI) and growing degree-days (GDD) based on daily average temperature threshold of 5°C have been calculated daily for Jackson and Moose climatological stations since 1949. Also, daily snow water equivalent (SWE) has been estimated for these stations using climatological records. Critical temperatures (-18°C for elk) have been summarized using departure from daily minimum temperatures. SWE, forage production, and critical temperatures are weighted and combined to determine Index of Winter Severity (IWS) for elk and bison.

Methods for calculating the IWS for elk and bison and how the IWS is used for Refuge operations will be presented. Average KBDI for different accumulations of GDD and spring precipitation are compared to production of grass and forbs on 34 different plant community groups. Methods and results for estimating forage production using KBDI, GDD, and precipitation are presented. **Key words: index, elk, bison, forage production**

048

Cole, G. F. 1972. Grizzly bear-elk relationships in Yellowstone National Park. Journal of Wildlife Management 36(2):556-561. Abstract: The elk (*Cervus canadensis*) population was mainly self-regulated by density-influenced mortality from intraspecific competition for food and compensating natality and survival. Mortality higher than usual was mainly due to weather that also increased the vulnerability of elk to predation by grizzly bears (*Ursus arctos*). Grizzly predation with competitive scavenging was a nonessential but assisting adjunct to other natural processes that regulated the elk population. As an interacting unit, bears of different social rank and an associated scavenger fauna probably helped to dampen elk population fluctuations by culling animals with low-energy reserves. The presence of a grizzly population in Yellowstone Park appears essential to have representative natural equilibriums among interacting secondary consumers, to maintain natural relationships between secondary and primary consumers, and to retain the scientific values of ecological systems with an intact native biota. **Key words: elk, predation, snow, temperature**

049

Compton, H. O. 1970. Southeastern Montana antelope population trends in relation to severe winters. Proceedings of the Antelope States Workshop 4:50-54. Summary: In the 1960s several severe winters (snow depths from 15 inches to 5 feet from November-February; temperatures of 0°F for 52 days, high winds and freezing conditions leading to hard, crusted snow) led to extensive shifts in range use. The following year antelope numbers region-wide were down 40% and fawn production was drastically reduced. Compton relates the mortality and production losses to an over-used range by large numbers of antelope followed by the severe winter conditions. Forage supplies were in poor condition due to over use and drought. Compton concludes the severe winter accelerated the downward trend brought about by an unbalanced antelope-range association. The hunting units showing the most depressed fawn crops and winterkill also showed loss of sagebrush to agricultural conversion. **Key words: antelope, snow, wind, temperature, productivity, mortality, nutrition, habitat use, drought, fecundity**

050

Conradt, L., T. H. Clutton-Brock, and F. E. Guinness. 2000. Sex differences in weather sensitivity can cause habitat segregation: red deer as an example. Animal Behaviour 59(5):1049-1060. Abstract: Sex differences in habitat use (habitat segregation) are widespread in sexually dimorphic ungulates. A possible cause is that males are more sensitive to weather than females, leading to sex differences in sheltering behaviour (the 'weather sensitivity hypothesis'). However, this hypothesis has never been tested. We considered the allometric rates of net energy gain during times of cold weather and food shortage in a model. We argue that the higher absolute head loses relative to intake rates of larger ungulates would indeed lead to higher weather sensitivity in males than in females. Furthermore, tested the weather sensitivity hypothesis empirically in red deer, *Cervus elaphus*, on the Isle of Rum, U.K. We predicted that (1) use of relatively exposed, high-quality forage habitat should be negatively influenced by bad weather; and (2) this influence should be stronger in males. We found that bad weather (strong wind, low temperature, heavy rain) in winter and spring influenced use of high-quality forage habitat negatively in all deer; that adult males responded more strongly to low temperature and strong wind than did females; and that adult males foraged on windy days at better sheltered sites than did females. Thus, the weather sensitivity hypothesis is supported both theoretically and empirically. We suggest that the weather sensitivity hypothesis can potentially explain winter habitat segregation in a large number of ungulate species. **Key words: red deer, habitat use, wind, temperature, precipitation**

051

Cook, D. B. and W. J. Hamilton, Jr. 1942. Winter habits of white-tailed deer in Central New York. Journal of Wildlife Management 6:287-291. The Adirondacks are characterized by a cold climate and deep snow. Deer therefore concentrate in evergreen swamps when the snow becomes deep enough to make travel difficult. In central New York, where the climate is milder and snow less deep, deer concentrate on steep south and southeast slopes regardless of cover type. Such slopes are sheltered from the

prevailing west wind and receive much sunlight. Snow is substantially less deep on such slopes. Wind and snow are the two factors which most affect the choice of deer winter range. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography,* University of BC, Vancouver, BC, Canada, p. 20.) **Key words: white-tailed deer, snow, habitat use, solar radiation**

052

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Society Wildlife Monographs No. 155, 64 pp. Abstract: Recent declines in numbers and juvenile recruitment in many elk (*Cervus elaphus*) herds in the western U.S. has sparked interest in factors that may cause these declines. Inadequate nutrition or delayed parturition, the latter of which may be caused by inadequate numbers of mature bulls (i.e., highly skewed sex ratios), may have separate or synergistic effects on population dynamics and productivity. We evaluated the implications of late parturition and summer-autumn nutrition on reproduction and survival of Rocky Mountain elk (*C. e. nelsoni*) using a captive herd of 57 cow elk.

We induced early (Sep.) and late breeding (Oct.) and 3 levels of summer-autumn nutrition on the cows. Food was offered *ad libitum* at 3 levels of digestible energy (DE): high = 2.9-3.0 kcal of DE/g of diets, medium = 2.6-3.0 kcal/g, and low = 2.3-3.0 kcal/g. Within these ranges, DE content was gradually reduced from late June through early November to mimic seasonal changes in the wild. During summer and autumn, we measured calf growth; body mass, nutritional condition, and breeding dynamics of cows; and growth and pregnancy of yearlings. We also measured carry-over (i.e., time-lag) responses including over-winter calf and cow survival and parturition date and birth mass, as functions of previous summer-autumn nutrition and previous parturition date. Between autumn 1995 and spring 1998, we conducted 2 years of parturition-date, summer-autumn nutrition experiments, 2 winters of calf survival experiments, and 1 winter of cow survival experiments.

Early birth provided calves with more time to grow before onset of winter. This 'head-start" advantage was maintained through late autumn, but its magnitude was diluted in some instances due to faster growth of some late-born calves. Body mass, body fat, and timing and probability of conception by cows in autumn were little influenced by parturition date the previous spring.

Summer-autumn nutrition significantly affected calves and their mothers. Growth of calves in the low and medium nutrition groups ceased by mid-September and late October. By December, calves in the high nutrition group were 40% and 70% heavier than calves in the medium and low groups, respectively. Cows in the high nutrition group accumulated about 75% and 300% more fat than cows in the medium and low groups by mid-October. Eighty percent of cows in the low nutrition group failed to conceive, and those in the medium group bred 10-14 days later than cows in the high group. Summer-autumn nutrition of calves influenced their probability of becoming pregnant as yearlings. Probability of pregnancy approached 100% for those yearlings that had high summer-autumn nutrition as calves and yearlings, despite near starvation their first winter of life.

Winter survival of calves was related to their size at the onset of winter. Smaller calves lost more body mass daily than did large calves, and thus they survived fewer days through winter. Summer-autumn nutrition largely determined calf body size at the

start of winter and, consequently, determined the proportion of winter survived. Survival of cows over winter was as related to body fat at the onset of winter as it was to nutrition during winter.

Carry-over effects of summer-autumn nutrition and parturition date on birth characteristics the following spring were minor. We detected no significant carry-over effect of summer-autumn nutrition or autumn condition on birth mass, although reduced condition in autumn delayed subsequent parturition date. Extent of body fat depletion in cows during the winter-survival experiments in 1998 accounted for 45% of the variation in parturition date. Ninety percent depletion delayed parturition an average of 34 days.

Delayed parturition, of a magnitude expected due to highly skewed sex ratios ($\leq$3 weeks under extreme conditions), probably has only a weak influence on vital rates of free-ranging elk. In contrast, fat accretion and probability of pregnancy of cows, and growth and overwinter survival of calves, were sensitive to small (10-20%) differences in DE content of food. Digestible energy levels of our 2 lower nutrition levels reflect DE ranges reported for large ungulate herds during summer and autumn in western North America. Thus, our data suggest that limiting effects of summer-autumn nutrition on populations may be greater than often assumed, perhaps greater than those during winter in some ecosystems, and consequently indicate a need for greater understanding of nutrition's influence on population dynamics and how this influence varies across space and time. To enhance further research, we present animal- and vegetation-based guidelines for evaluating nutritional influences on elk populations. **Key words: elk, nutrition, population dynamics, parturition**

053

Cormie, A. B. and H. P. Schwarcz. 1999. Effects of climate on deer bone ƃ^{15}N and ƃ^{13}C: Lack of precipitation effects on ƃ^{15}N for animals consuming low amounts of C_4 plants. Geochimica et Cosmochimica Acta 60(21):4161-4166. Abstract: We have examined the relationship of bone collagen ƃ^{15}N and ƃ^{13}C to climatic variables, humidity, temperature, and amount of precipitation using fifty-nine specimens of North American white-tailed deer (*Odocoileus virginianus*) from forty-six different locations. In previous studies of African mammals there was a significant correlation between bone collagen ƃ^{15}N and local amount of precipitation. Results presented here similarly show an increase in ƃ^{15}N with decreasing amount of precipitation but only for 25% of the animals, namely those consuming more than 10% C_4 plants. These animals also exhibited a significant correlation between ƃ^{13}C and temperature which mirrors previous observations for grasses suggesting that these deer consume grasses during times of population and nutrient stress.

In contrast, even in dry areas containing high proportions of C_4 grasses, the majority of the deer had consumed low amounts of C_4 plants and these deer did not have ƃ^{15}N which correlate with amount of precipitation. Only when deer deviated from their normal feeding pattern by consuming C_4 plants or grasses did their ƃ^{15}N correlate with amount of rainfall. For these animals, consumption of C_4 plants or grasses may signal conditions of water and nutrient stress. An increase in ƃ^{15}N of bone collagen may result from combined effects from excretion of concentrated urine (to conserve water) and increased internal recycling of nitrogen (to conserve nitrogen). **Key words: white-tailed deer, precipitation, nutrition**

054

Corp, N., A. Spalton, and M. L. Gorman. 1998. The influence of rainfall on range in a female desert ungulate: the Arabian oryx (*Oryx leucoryx*) in the Sultanate of Oman. Journal of Zoology London 246:369-377. Abstract: In this study we investigated the effect of rainfall on the home range (calculated over 90 days) of adult female Arabian oryx (*Oryx leucoryx*) in a reintroduced population in central Oman. We looked at response to rainfall for six rain events in the period June 1986 to January 1992; rainfall was localized on five occasions and on one occasion covered the study area. Response, in terms of range and core area, showed considerable variation between rainfall events, perhaps as a result of variation in ranging behaviour between individual oryx. However, in the first 90 days after localized rainfall the home range and core area of oryx outside rain areas increased before decreasing significantly 91-108 days after rain. In comparison, range and core area of oryx inside areas of localized rainfall either did not change or decreased after rainfall as animals took advantage of improved conditions locally rather than investigating grazing elsewhere. When rain fell over the whole study area, range size did not change, but there was an immediate increase in core area and a reduction in range overlap indicating movement to new areas. During extended drought very localized rainfall caused oryx to move quickly to areas of new rain and by 28 days 70% of all adult females had found fresh grazing. Thereafter numbers declined to around 30% by 225 days, before oryx again moved back in to the new rain areas. We attributed this pattern of movement to changes in the nutritional quality, measured as crude protein, of available forage. Data for single animals revealed considerable individual variation in response to rainfall; some animals moved quickly to rain whilst others failed to reach it. This variation has consequences for reproductive success and survival and illustrated that, of the oryx, response to rainfall is a key to desert success. **Key words: oryx, precipitation, drought, behavior**

055

Coughenour, M. B. and F. J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecological Applications 6(2):573-593. Abstract: The interrelations of weather, plant production and abundance, and elk population dynamics on Yellowstone's northern winter range were examined for a 23-year period when there was minimal human offtake from the herd. Significant correlations between precipitation and plant production, between elk population responses and precipitation, and between elk population responses and elk population density strongly suggested that forage limited elk population growth. Although population responses to density have been documented previously in Yellowstone, responses to precipitation have not. Correlations between elk population responses and annual precipitation were presumably consequences of plant growth responses to precipitation and subsequent effects on elk nutritional status. Population regulation was most consistently achieved through the responses of juveniles rather than adults. Winter mortality of juveniles was primarily correlated with elk numbers, whereas recruitment was primarily correlated with precipitation. Adult mortality rates were not significantly correlated with elk numbers, but were correlated with precipitation. Per capita rate of increase was negatively correlated with elk number, but 55% of the variance was density-independent. There was evidence that winter weather affected the elk, but season-long weather indices had poor predictive power. A stage-structured population

model using regression equations of mortality and recruitment rate responses to precipitation and elk numbers, predicted that the population could vary within a range of ~16,400 ± 2500 sighted elk (mean ± 1 SD). **Key words: elk, precipitation, population dynamics, nutrition, mortality**

056

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather and population crashes in Soay sheep. Science 292(5521):1528-1531. Abstract: Quantifying the impact of density, extrinsic climatic fluctuations, and demography on population fluctuations is a persistent challenge in ecology. We analyzed the effect of these processes on the irregular pattern of population crashes of Soay sheep on the St. Kilda Archipelago, United Kingdom. Because the age and sex structure of the population fluctuates independently of population size, and because animals of different age and sex respond in different ways to density and weather, identical weather conditions can result in different dynamics in populations of equal size. In addition, the strength of density-dependent processes is a function of the distribution of weather events. Incorporating demographic heterogeneities into population models can influence dynamics and their response to climate change.

Survival of lambs and older females (.6 years) was negatively associated with density, whereas survival of prime adults and female yearlings was not related to density. Survival rates of lambs and males were influenced by weather throughout winter [the winter North Atlantic Oscillation (NAO)(16)], whereas survival rates of yearlings and prime adult females were most strongly influenced by rainfall at the end of winter (17). In each age and sex class, survival rates were lower in wet, windy winters (high NAO values). Density and weather interacted and bad weather depressed survival rates at high density. The strength of the interaction was greatest in young and old animals. **Key words: Soay sheep, density, mortality, NAO, precipitation**

057

_____, E. J. Milner-Gulland, and T. Clutton-Brock. 2000. The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. Proceedings of the Royal Society of London B 267:1771-1779. Summary: The relative influences of density-dependent and –independent processes on vital rates and population dynamics have been debated in ecology for over half a century, yet it is only recently that both processes have been shown to operate within the same population. However, generalizations on the role of each process across species are rare. Using a process-orientated generalized linear modeling approach we show that variations in fecundity rates in populations of three species of ungulates with contrasting life histories are associated with density and winter weather in a remarkably similar manner. However, there are differences and we speculate that they are a result of differences in size between the species. Much previous research exploring the association between vital rates, population dynamics and density-dependent and -independent processes has used pattern-oriented approaches to decompose time-series into contributions from density-dependent and –independent processes. Results from these analyses are sometimes used to infer associations between vital rates, density and climatic variables. We compare results

from pattern-orientated analyses of time-series with process-orientated analyses and report that the two approaches give different results. The approach of analyzing relationships between vital rates, density and climatic variables may detect important processes influencing population dynamics that time-series methodologies may overlook. **Key words: Soay sheep, Saiga antelope, red deer, population dynamics, model**

058

Coulson, T. N., S. D. Albon, J. M. Pemberton, J. Slate, F. E. Guinness, and T. H. Clutton-Brock. 1998. Genotype by environment interactions in winter survival in red deer. Journal of Animal Ecology 67:434-445. Summary: (1) The extent to which environmental heterogeneity interacts with genetic heterogeneity to affect individual fitness within populations has the potential to affect the dynamics of natural populations and the amount of genetic variation maintained in natural populations, yet is a relatively poorly investigated topic in either ecology or evolutionary biology. (2) Many individual-based studies are precluded from such investigations by the practical problems of measuring heritability of traits affecting fitness and the difficulties of experimental manipulation of the study population. One way of demonstrating how commonly genotype by environmental interactions affect fitness, though not their overall importance in determining fitness, is to investigate fitness in a population subdivided by genotype at one or more marker loci. (3) We analyzed data on calf winter survival from a population of red deer from the Isle of Rum, Scotland. Data on individual survival, environmental fluctuations and genotype at 13 loci were collected from 1982 to 1994. (4) We found associations between survival over the first winter of life and calf genotype at two out of three allozyme loci and five out of 10 microsatellite loci. All of the results remained significant under randomization tests. Other genotypes that initially appeared to have an association with survival were rejected when bootstrapped, usually due to insufficient data or anomalies in the data. (5) Our results suggest that associations between fitness and genotype are common. Five out of the seven associations found involved interactions with environmental variables. Four of these showed density-dependent selection with different genotypes showing high survival at high population size compared to low population size and one interacted with autumn rainfall. In a sixth case, genotype interacted with sex. **Key words: red deer, genetics**

059

Cowan, I. McT. 1950. Some vital statistics of big game on overstocked mountain range. North American Wildlife Conference 15:581-588. Summary: Cowan describes the impact of winter range overcrowding by multiple species including mule deer, moose, bighorn, and elk. Malnutrition in the study area was periodically intensified by severe winter weather in the form of heavy snow and low temperatures. This confluence profoundly influenced fecundity (survival of young to yearling class) and sex ratio. The author states his data suggests overcrowding acts more severely on mature males than females. Losses of elk calves was high during their first winter under overstocking. Bighorn appeared more vulnerable to conditions of a severe winter of unusual snow and intense cold resulting in low yearling survival. Sex ratios among adult animals favored females in all species except moose; effective reproduction of all species was low. Elk, goat and bighorn lost a greater proportion of short yearlings. Mule deer also produced a

much smaller year class of fawns the following spring resulting in doubling of the loss. **Key words: wild sheep, elk, mule deer, moose, sex ratio, nutrition, snow, temperature**

060

Craighead, J. J., F. C. Craighead Jr., R. L. Ruff, and B. W. O'Gara. 1973. Home ranges and activity patterns of nonmigratory elk of the Madison Drainage herd as determined by biotelemetry. Wildlife Management Monograph 33:1-50. Elk in Yellowstone wintered in thermal areas where snow depths were minimal. Winter movements were so restricted that no animal was observed to more >1 airline mile in 24 hr. Elk moved into surrounding lodgepole pine forest to feed but never moved through 4-5 ft snow cover for more than 300 yards.(Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver, BC, Canada, p. 20.) **Key words: elk, snow, movement**

061

Crête, M. 1976a. Estimation of winter mortality of deer in Quebec. Canadian Field Naturalist 90(4):397-403. Abstract: Snow depth, snow compaction, deviation of the minimum and maximum temperatures from the general mean, deer track density, proportion of trails, sinking depth of deer in snow, the average diameter of the twigs at the point of browsing (dpb) of the most important deciduous shrub species and the area covered by the deer yard were measured every 2 weeks in a deer wintering area during the winters of 1973-1974 and 1974-1975. The mean dpb was used to estimate the quality of the deer browse. A multiple regression analysis revealed that the dpb variation through the winter was related to the sinking depth of the deer in snow, to the time elapsed since the beginning of the winter, to the deviation of the minimum temperature from the general mean, and to the snow depth. I hypothesize that the quality of food ingested by deer, as estimated by the dpb, is related to the winter mortality of deer. Correlation coefficients were computed between the mean dpb and (1) the total number of deer found dead during the same period of time, (2) the number of deer dead from predation during this time interval, (3) the marrow fat content of those carcasses, and (4) the proportion of fawns among the carcasses. Only the last was significant in 1973-1974, whereas the first three were significant in 1975. A comparison between the number of carcasses found during each 2-week interval and each measurement taken in the deer yards showed that the dpb of all the measurements taken in the yards was the best index of deer winter mortality. The use of the dpb as an index of winter mortality could possibly be extended to all the deer range in Quebec. **Key words: white-tailed deer, snow, nutrition, mortality, movement, index**

062

_____. 1976b. Importance of winter climate in the decline of deer harvest in Quebec. Canadian Field-Naturalist 90:404-409. The effect of the mean winter temperature and the total snowfall and rainfall in winter on the Quebec deer harvest was studied by means of a multiple regression analysis. The period from 1963 to 1973, when a marked crash occurred in the deer harvest, is covered by the analysis. As the length of the hunting season varied considerably during this time interval, it was also included in

the statistical analysis. The length of the deer season eliminated about 80% of the variation of the deer harvest in three regions of the deer range and accounted for 58 and 31% of the harvest fluctuation in the remaining two. The combined effect of the meteorological variables seemed to explain between 5 and 20% of the total harvest variation representing about half of the remaining harvest fluctuation. On the south shore of the St. Lawrence River, snow depth and its supporting quality modified by rainfall were often related to the deer harvest of the next season. On the north shore, mean winter temperature seemed to act upon the snow supporting quality instead of rain. The unexplainable part of the harvest variation could mainly depend on the reduction of the summer and winter habitat, on overharvesting, on predation, and on summer and fall weather conditions. **Key words: deer, snow, precipitation, mortality**

063

Cross, P. C., W. H. Edwards, B. M. Scurlock, E. J. Maichak, and J. D. Rogerson. 2007. Effects of management and climate on elk brucellosis in the greater Yellowstone ecosystem. Ecological Applications 17(4):957-964. Abstract: Every winter, government agencies feed ~6000 metric tons ($6x106^2$ kg) of hay to elk in the southern Greater Yellowstone Ecosystem (GYE) to limit transmission of *Brucella abortus*, the causative agent of brucellosis, from elk to cattle. Supplemental feeding, however, is likely to increase the transmission of brucellosis in elk, and may be affected by climatic factors, such as snowpack. We assessed these possibilities using snowpack and feeding data from 1952 to 2006 and disease testing data from 1993 to 2006. Brucellosis seroprevalence was strongly correlated with the timing of the feeding season. Longer feeding seasons were associated with higher seroprevalence, but elk population size and density had only minor effects. In other words, the duration of host aggregation and whether it coincided with peak transmission periods was more important than just the host population size. Accurate modeling of disease transmission depends upon incorporating information on how host contact rates fluctuate over time relative to peak transmission periods. We also found that supplemental feeding seasons lasted longer during years with deeper snowpack. Therefore, milder winters and/or management strategies that reduce the length of the feeding season may reduce the seroprevalence of brucellosis in the elk populations of the southern GYE. K**ey words: elk, disease, snow**

064

Dailey, T. V. and N. T. Hobbs. 1989. Travel in alpine terrain: energy expenditures for locomotion by mountain goats and bighorn sheep. Canadian Journal of Zoology 67:2368-2375. Abstract: We used indirect calorimetry to measure energy expenditure for locomotion by three mountain goats (*Oreamnos americanus*) and five bighorn sheep (*Ovis canadensis*) in response to variation level of activity, slope of travel, and snow conditions. The energetic increment of standing over lying averaged 26% of the two species. We could detect no difference between species in the net cost of travel on level surfaces (line over x = 0.26 mL O_2/(g · km)). Energy expended by bighorn sheep and mountain goats for lifting 1 kg of body weight one vertical meter on a 21.5° slope (ca. 37 J/(kg · m)) exceeded the highest cost documented for quadrupeds. Energy expended walking down a 21.5° slope exceeded energy expenditure for horizontal locomotion, or was recovered inefficiently (ca. 25% recovery of potential energy). The

relative increase in the net cost of locomotion in snow achieved an asymptote when sinking depth exceeded 1.2-2.0 times brisket height. The slope of the relative increase in the net cost of locomotion as a function of sinking depth=brisket height was lower for mountain goats than for any North American ungulate studied to date. Consequently, mountain goats were less efficient than other species when snow was shallow, but were more efficient when it was deep. We explain this result on the basis of interspecific differences in locomotory behavior and foot loading. **Key words: wild sheep, mountain goat, bioenergetics, snow**

065

Daleszczyk, K., M. Krasinska, Z. A. Krasinski, and A. N. Bunevich. 2007. Habitat structure, climatic factors, and habitat used by European bison (*Bison bonasus*) in Polish and Belarusian parts of the Bialowieza Forest, Poland. Canadian Journal of Zoology 85(2):261-272. Abstract: Bialowieza Forest is divided into Polish and Belarusian parts that differ in habitat structure and degree of protection. The forest supports two European bison, *Bison bonasus* (L., 1758), populations that are isolated from each other. We analyzed bison habitat use from relocations of 34 radio-collared bison from both populations collected in 1993-2003. The two bison populations differed considerably in habitat use, but home-range sizes were similar. The habitat structure in the Polish part is more advantageous for bison (deciduous forests prevail) than in the Belarusian part; however, open areas form a rich source of forage for ungulates in the Belarusian part, which presumably helped to eliminate the difference between the two parts. In 1977-2003, the annual temperature in this area rose and the total precipitation diminished. As a result, the habitat use by bison changed in both populations when compared with those in earlier studies; use of coniferous forests decreased, while use of deciduous forests and alderwoods increased. Generalized linear models on relationships among climatic factors and habitat use showed that the amount of water accessible in the period up to 4 years ago was the main factor affecting the use of various forest types. Habitat preferences differed between adult bulls and groups that included cows, but were similar in both populations irrespective of the differences in habitat composition. **Key words: bison, precipitation, habitat use, temperature**

066

Darimont, C. T., P. C. Paquet, T. E. Reimchen, and V. Crichton. 2005. Range expansion by moose into coastal temperate rainforests of British Columbia, Canada. Diversity and Distributions 11:235-239. Abstract: Ranges of species are dynamic and respond to long-term climate change and contemporary effects such as habitat modification. We report here that moose (*Alces alces*) have recently colonized coastal temperate rainforests of British Columbia, Canada. Contrary to recent publications, field observations of moose and their sign, combined with their occurrence in wolf (*Canis lupus*) faeces, suggest that moose are now widespread on the coastal mainland and occur on least three islands. Traditional ecological knowledge (information accumulated by aboriginal peoples about their environment) suggests that colonization occurred during the mid 1900s, concomitant with logging of major watersheds that bisect the Coast Mountain Range. Range expansion by moose may have ecological consequences such as alteration of predator-prey dynamics and transmission of disease to native deer (*Odocoileus hemionus*). **Key words: moose, habitat use, disease**

067

Darling, F. F. 1937. A herd of red deer. Oxford University Press, London. Notes: The author discusses meteorological factors in red deer movement including temperature, humidity, wind, rainfall, snow and frost, which he identifies as instigators of movement. He notes that deer are often affected by sharp alterations of temperature when they seek more even conditions, causing them to inhabit lower areas and to gather or 'flock'. If conditions are sufficiently 'bad', daily movement is restricted. When daily maximum and minimum temperatures are widest, red deer moved over a greater range. Darling found frost may check movement or evoke it, depending on the degree of humidity and ground conditions. Darling found the humidity of the atmosphere to have the most potent influence on movement in deer; high atmospheric humidity tends to restrict day-to-day movement and dry atmosphere induces it. He found high and variable humidity makes for constant olfactory stimulation which renders deer more easily disturbed; a warm, moist atmosphere is a better conductor for scent than a dry one or a cold moist one. The author did not find wind to be one of the most potent influences on movement, but interacts with other environmental factors to generate movement. He found precipitation in the form of a steady rain tends to restrict movement. Deer are highly influenced by the coming of snow, often flocking two or three days ahead of a storm. Related meteorological events include a drop in relative humidity and a north wind. During snow the red deer frequently made use of long heather as it provided easier access to food. Reproductively, cold dry nights mean intense sexual activity. However humid air and clouds result in very little roaring accompanied by decreased physical activity. **Key words: red deer, temperature, humidity, snow, wind, movement**

068

Dasmann, R. F. and W. P. Dasmann. 1963. Mule deer in relation to a climatic gradient. Journal of Wildlife Management 27(2):196-202. Abstract: A comparison of mule deer (*Odocoileus hemionus*) populations and their habitats occurring along a climatic gradient from humid coastal forest through chaparral to sagebrush reveals differences in soils, quality of forage, plant successional rate, and animal numbers. These differences determine the usefulness of fire, mechanical treatment, or other disturbance of climax vegetation for improving deer habitat. They also affect the degree of control which must be exercised over big game numbers. The protein content of deer forage tends to follow the climatic gradient. In general, soils of the more humid vegetation regions produce less protein and hence support fewer, and smaller, deer in permanent populations than do the soils of less humid regions. Although protein content of deer forage can be increased by burning in these humid regions, the increase is only temporary. Fire, logging, or other means of removing climax vegetation and starting successional growth favor deer in the coastal forest and chaparral by increasing the amount and the protein content of forage. In the arid sagebrush, however, such disturbances are usually detrimental. The high value of timber in most of the coastal forest prohibits direct management for deer, and deer are a temporary crop following logging. Chaparral and sagebrush, however, can be managed for the production of deer as a primary crop. **Key words: mule deer, nutrition, humidity**

069

DelGiudice, G. D., M. R. Riggs, P. Joly, and W. Pan. 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. Journal of Wildlife Management 66(3):698-717. Abstract: Knowledge of age-specific survival of deer (*Odocoileus* spp.) and the underlying causes of mortality are essential to our understanding of their population dynamics. We examined age-specific survival and cause-specific mortality of female white-tailed deer (*O. virginianus*) in an area where wolves (*Canis lupus*) recently had become reestablished and assessed the influence of winter severity during 1991-1996 using new survival analysis procedures. Sufficient data permitted rigorous survival analyses on 153 of 179 radiocollared females ≥0.6 years old, whose age distribution remained stable with annual median ages of 5.9-6.7 years old during the last 5 years of the study. Winter severities ranged from unusually mild to historically severe; 84% (81 of 97) of all mortalities occurred during November-May. The median age of deer survival according to the iterative Nelson estimator (INE) was 3.6 years (90% confidence limits [CL] = 2.4, 4.0). The smoothed estimate of the hazard function was a U-shaped curve with an elevated risk of mortality at 0.6 years old, which declined progressively until 5 years old, then increased steadily with the highest age specific risk of death for deer ≥ 10 years old. Fits of the Anderson-Gill (AG) proportional hazards model to our data indicated that survival was negatively associated (P<0.0001) with winter severity (primarily snow depth), but not with site of winter capture or body mass at capture. The risk of death increased progressively over the course of each winter, with maximum risk occurring in winters of greatest snow depth. Estimated life-time mortality rates (90% CL) due to hunting, wolf predation, and miscellaneous causes were 43.3% (29.5, 57.1%), 33.1% (20.1, 45.3%), and 23.6% (13.2, 34.0%), respectively. Within 5-11 years of reestablishment in our area, wolf predation became a leading cause of mortality for female deer, but its importance relative to hunting depended on annual fluctuations in winter severity. Competing risk analyses permitted comparison of age-specific hazards associated with hunter harvest, wolf predation, and miscellaneous causes of mortality. The nature of the observed interaction between the cause-specific hazards and the effects of winter severity appears to validate the practice of regulating the issuance of antlerless deer permits based on population conditions. Collective evidence suggests that as agencies formulate management strategies relative to wolf reintroduction or range expansion, the frequency of severe winters, snow depth, deer population goals, and the use of antlerless permits should be primary considerations. **Key words: white-tailed deer, snow, mortality, predation**

070

_____, R. A. Moen, F. J. Singer, and M. R. Riggs. 2001. Winter nutritional restriction and simulated body condition of Yellowstone elk and bison before and after the fires of 1988. Wildlife Monographs No. 147, The Wildlife Society. Abstract: We collected and chemically analyzed urine in snow (snow-urine) and simulated physiology of elk (*Cervus elaphus*) and bison (*Bison bison*) at the population level to assess changes in nutritional restriction, physical condition (i.e., fat reserves), and mortality rates on the Northern and Madison-Firehole ranges and at Pelican Valley in Yellowstone National Park during winters 1987-88 (1988) to 1989-90 (1990). On the Northern and Madison-Firehole ranges, elk diets varied over the 3 winters with lowest

consumption of grasses ($P \leq 0.006$) and highest consumption of conifers ($P \leq 0.044$) during the first winter post-fire (1989), which was also the most severe winter with respect to snow depth. Sedge used by Northern range elk also varied ($P \leq 0.002$) with lowest use during prefire winter 1988 and greatest use during winter 1990; sedge use was stable at the more thermally-influenced Madison-Firehole range. Decreasing ($P \leq 0.014$) mean urinary potassium:creatinine (K:C) ratios reflected progressive nutritional restriction on all sampling areas during all 3 winters. Mean urinary urea nitrogen:creatinine (UN:C) ratios of elk varied ($P < 0.001$) on the lower, middle, and upper Northern range and at Madison-Firehole during all 3 winters, except on the lower Northern range during winter 1989. Values of mean UN:C ratios and temporal trends indicated nutritional restriction was greatest during winter 1989, and restriction was increasingly severe from the lower to upper elevations of the Northern range and most severe at Madison-Firehole, where snow depths were greatest.

On the Northern and Madison-Firehole ranges, bison use of grasses decreased ($P \leq 0.006$) and sedges increased ($P \leq 0.005$), while conifer use remained low and stable throughout the study. In Pelican Valley, bison food habits were unaltered during the study. Bison and elk diets were more similar at Madison-Firehole than on the Northern range, suggesting greater competition for food at Madison-Firehole. Mean K:C ratios of bison declined ($P \leq 0.014$) throughout all winters on all sampling areas. Mean UN:C ratios increased ($P \leq 0.030$) on the Northern, Madison-Firehole, and Pelican Valley ranges in each winter. Mean UN:C ratios were lower in bison than in elk, but temporal trends indicated that nutritional restriction of bison progressively increased each winter and was most severe during winter 1989.

Measured UN:C ratios and herd composition were used by the physiological model to predict DEI on each range for bison and elk. At the predicted DEI on each range, there were spatial and temporal differences in fat reserves and mortality rates of elk and bison. The physiological model predicted that Madison-Firehole elk and bison were more severely nutritionally restricted and had lower fat reserves during winter 1989 than elk and bison on the Northern range. Lower fat reserves and higher winter mortality rates of elk and bison calves compared to cows predicted by the physiological model were consistent with the differential pressure exerted by density-dependent factors and amplified during the more severe winter. **Key words: elk, bison, drought, nutrition, snow, diet**

071

_____, R. O. Peterson, and W. M. Samuel. 1997. Trends of winter nutritional restriction, ticks, and numbers of moose on Isle Royale. Journal of Wildlife Management 61(3):895-903. Abstract: During a 7-year study, we monitored winter nutritional restriction of moose (*Alces alces*) and moose numbers on Isle Royale (winters 1987-88 to 1993-94). Over the 7 winters, the estimated moose population decreased 26% from an historic high of 1,653 (winter 1987-88) to 1,216 (1989-90), then increased to a new high (1,880 and 1,770) by winters 1992-93 and 1993-94. During that time, there was a significant ($P = 0.0486$) negative relation ($r = -0.84$) between the percent of urine specimens collected from snow (snow-urine) in late winter with urea nitrogen:creatinine (UN:C) ratios ≥ 3.5 mg:mg and percent change in the moose population from winter 1987-88. Mean urinary UN:C of moose residing on the east and west ends of Isle Royale declined ($P \leq 0.0001$) among years; however, slopes of the 2 trends were different ($P =$

0.0001). The nutritional restriction and decline in moose numbers appeared to involve an epizootic of the winter tick (*Dermacentor albipictus;* indicated by percent moose observed with tick-induced hair breakage and loss). During winters 1987-88 to 1989-90, the percentage of late winter snow-urine specimens with UN:C ratios indicative of severe nutritional restriction ranged from 47 to 58%; however, the percentage decreased to zero by winter 1993-94 as the tick infestation subsided and moose numbers increased. **Key words: moose, insects, index, mortality, nutrition**

072

D'Eon, R. G. 2003. Snow depth as a function of canopy cover and other site attributes in a forested ungulate winter range in southeast British Columbia. British Columbia Journal of Ecosystems and Management 3(2):66-78. Abstract: Snow depth is considered a major influence on deer (*Odocoileus* spp.) winter distribution and abundance in northern parts of their range. Overstorey canopy cover is often considered a principal variable governing snow depths in forests and has implications for managers who wish to achieve reduced snow depths by manipulating canopy closure in forests. I used three years of snow-depth data collected in forested ungulate winter range in southeast British Columbia to determine the relative influence of canopy closure and other site attributes on snow depth. Although canopy closure was a major factor in determining snow depth, it was outweighed by elevation and aspect. I found a close relationship between canopy closure and snow depth at low-elevation sites, but this relationship diminished or disappeared at higher elevations and on cooler aspects supporting the hypothesis that the influence of canopy closure depends on overall snow accumulation. At low elevations, forest managers could use canopy closure to influence snow depths. I offer the generalization that, on similar sites, maintaining 50% canopy closure will reduce snow depths by approximately 20%; 100% canopy closure will reduce snow depths by up to 40%. **Key words: deer, snow, habitat use**

073

Des Moules, P. 1964. The influence of snow on the behaviour of moose. Transactions Northeast Wildlife Conference 21(1):1-17 and Pages 51-68 *in* Traveux en Cours en 1963. Rapport No. 3, Service de la fauna du Quebec, Ministre du Tourisme. A study of the effect of snow on moose in Laurentides Provincial Park, Quebec. Cross-sections of typical quamaniq depressions are shown for balsam fir and white birch. Snow depths under various canopy types are presented. In early winter, moose bedded in deep snow areas (cut-over hardwoods). As snow depth increased, beds were found increasingly often under more closed canopies. At snow depths of 30-34 inches, moose shifted activity from cut-over areas to small- or medium-sized openings. They rarely entered areas with more than 42-48 inches of snow. The deeper the snow, the more restricted the moose became to quamaniqs. This resulted in a shift to coniferous browse. As snow depth increased, moose broke up into smaller groups. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver, BC, Canada p. 21.) **Key words: moose, snow, behavior**

074

DeVos, J. C. Jr. and W. H. Miller. 2005. Habitat use and survival of Sonoran pronghorn in years with above-average rainfall. Wildlife Society Bulletin 33(1):35-42. Abstract: Sonoran pronghorn (*Antilocapra americana sonoriensis*) occur in an arid desert in northwestern Sonora, Mexico and southwestern Arizona; their numbers have declined since 1920. Causes of the decline are largely speculative but include habitat alteration by humans, excessive herbivory by domestic livestock, illegal harvest, and exposure to domestic livestock diseases. We initiated this study to develop information on habitat use and survival to aid in developing recovery strategies for Sonoran pronghorn. We captured 19 Sonoran pronghorn and monitored their movements and habitat use patterns from 1983 through 1991 and compared these locations to random locations to assess habitat use. We also calculated survival. Sonoran pronghorn used the creosote bush (*Larrea tridentata*) – white bursage (*Ambrosia dumosa*)-paloverde (*Parkinsonia* spp.)-mixed cacti association greater than expected. Locations of Sonoran pronghorn close to water occurred more frequently than random locations, and areas farthest from waters were used less than expected. Sonoran pronghorn used areas within 1 km of roads less than random locations and use locations >1 km from roads as expected or greater than expected as distance from roads increased. Mean annual estimated survival for females and males was 0.96±0.04 and 0.92±0.04, respectively. Sonoran pronghorn had very low mortality rates and the population expanded to levels that likely have not occurred since the 1920s. **Key words: mortality, precipitation, habitat use, antelope**

075

Dolbear, A. E. 1897. The cricket as a thermometer. American Naturalist 31(371):970-971. Abstract: The rate of cricket chirps seem to be entirely determined by the temperature and this to such a degree that one may easily compute the temperature when the number of chirps per minute is known. Thus at 60°F the rate is 80 per minute. One may express this relation between temperature and chirp rate thus: Let T stand for temperature and N, the rate per minute:T=50+N-40/4. **Key words: insects, temperature, index**

076

Douglas, C. L. 2001. Weather, disease, and bighorn lamb survival during 23 years in Canyonlands National Park. Wildlife Society Bulletin 29(1):297-305. Abstract: The Island-in-the-Sky desert bighorn herd (*Ovis canadensis nelsoni*), the largest in Canyonlands National Park, Utah, is used extensively by Utah Division of Wildlife Resources to re-establish herds in former habitat throughout the state. This study was undertaken because Park managers became concerned about delayed herd recovery following 4 years of transplant removals and suspended trapping operations. This concern led to my study of effects of weather on yearly lamb:ewe ratios for the Park's 23-year database. I used weather variables regulating the annual growing season, soil-moisture regime, and body condition of ewes to develop multiple-regression models. Regression models, developed from 10 and 16 years of data, explained 91% and 61% of the variation in lamb:ewe ratios, respectively; I estimated lamb:ewe ratios for remaining years of data and compared them with observed values. Maximum ambient

temperatures in May of the same year lambs were born and precipitation from January through March 2 years before lambs were born (thought to relate to body condition of ewes) were variables correlated most strongly with lamb:ewe ratios. Peak of lambing occurs in April and May. May is the pivotal month, which, on average, has maximum temperatures that promote negative soil-moisture storage and a decrease in forage nutrients. Disease (contagious ecthyma) was first noticed in 1986 and apparently reduced lamb survival through 1992. I used data from disease years to estimate lamb survival, but not for model development. **Key words: wild sheep, model, mortality**

077

_____**and D. M. Leslie, Jr. 1986. Influence of weather and density on lamb survival of desert mountain sheep. Journal of Wildlife Management 50(1):153-156.** Abstract: This report concerns the effect of weather on lamb survival in desert mountain sheep (*Ovis canadensis nelsoni*) to 6-8 months of age in the River Mountains, Nevada, and how it integrates with density to limit the population. Regression analyses were used to examine relationships between lamb survival and weather variables from 1970 to 1982. Autumn precipitation (Sep-Dec) of the preceding year (during gestation) had a significant (P<0.05), positive effect on lamb survival. Herd density was significantly (P<0.05) and inversely related to lamb survival. Spring winds had a positive and significant (P<0.05) effect on lamb survival. Multiple regression revealed that 87% of the variability in lamb survival was accounted for by autumn precipitation during gestation (52%) and sheep density (35%). **Key words: precipitation, wind, wild sheep**

078

Drimmer, F., editor. 1954. The Animal Kingdom. Volume II. Greystone Press – Hawthorn Books, New York. Notation: “Though the coyote, wolf, cougar, and eagle are among the pronghorn’s natural enemies, snow is its most dreaded foe of all. Deep snow deprives the pronghorn of its natural food supply—grasses, brush and the like. Moreover, it causes the animal to founder as it attempts to forage. At the same time, deep snow drives the wolves and coyotes frantic with hunger. During excessively cold and snowy winters, pronghorns starve to death by the thousands. During the fearful winter of 1893, when the temperature fell to 61° below zero at Fort Assiniboine, Montana, nine hundred antelope perished in deep snow drifts near the post.” (page 762). **Key words: antelope, snow, temperature, mortality**

079

Drolet, C. A. 1976. Distribution and movements of white-tailed deer in southern New Brunswick in relation to environmental factors. Canadian Field-Naturalist 90:123-136. White-tailed deer (*Odocoileus virginianus*) were marked and followed by telemetry between December 1969 and May 1972 to determine their seasonal home ranges, distribution by forest cover types, and their movements in response to snow depth, precipitation, barometric pressure, temperature, wind, windchill, and time of day. Twenty-eight deer were radio-equipped and 22 (12 adults, 5 yearlings, and 5 fawns) were relocated. Sizes of home ranges were measured by computerized movement maps: 949 ha for three deer in a snowfree winter; 88 ha for seven deer in a winter of deep show, 341 ha for five deer in a winter of average snowfall, and 266 ha for five deer

in two summers. In a winter of deep snow, the area used declined to 7.3% and distance traveled per hour to 76% of their respective values in a snowless winter. Windchill, barometric pressure, and temperature had less effect on deer movements as snow accumulated. Deer moved mostly in later afternoon evenings and early morning in winter, and mid-day and evening at other times of the year. Relocations indicated a preference of deer for mixedwood cover throughout the year, but as snow accumulated use of softwood increased. Deer moved to winter ranges when snow accumulated to 30 cm in hardwood stands and returned to summer ranges after several days of temperatures above 5.5° C. Some deer moved up to 20 km from summer to winter ranges. Improved interspersion obtained by modifying sylvicultural practices could provide ample winter habitat in areas considerably smaller than the 300-400 ha measured. Areas of 300-400 ha with many small clear-cuts provided adequate summer habitat. **Key words: white-tailed deer, snow, temperature, wind, precipitation, barometric pressure, movement, distribution, habitat use**

080

Dunham, K. M., E. F. Robertson, and C. C. Grant. 2004. Rainfall and the decline of a rare antelope, the tsessebe (*Damaliscus lunatus lunatus*) in Kruger National Park, South Africa. Biological Conservation 117:83-94. Abstract: The number of tsessebes in Kruger National Park, South Africa, increased during 1977-1985, but declined after 1986. We used tsessebe number and age structure to determine year-to-year variation in adult survival. Adult survival rate was positively correlated with dry-season rainfall (a measure of grass productivity during the dry season) and with the cumulative rainfall surplus. Juvenile survival rate (as indexed by the juvenile:female ratio) was also correlated with the cumulative rainfall surplus. Tsessebe feed in broad, grass-covered drainage lines within *Colophospernum mopane* shrublands on basaltic soils. Here drainage is slow and the cumulative rainfall surplus or deficit, relative to the mean annual rainfall, is an index of dry-season soil moisture, which, in turn, determines dry-season grass productivity and hence the food supply for tsessebe. Adult survival rate was density-dependent, indicating that there was intraspecific competition for food. When the relationships between survival rates and rainfall were used in a model of tsessebe population dynamics to predict juvenile and adult survival rates from the recorded annual and dry-season rainfalls, the modeled population changes were similar to those observed. We conclude that changes in tsessebe numbers probably resulted from rainfall-induced changes in food availability during the dry season, which caused adult survival to decline after 1986. The principal management implication is that the tsessebe decline can be reversed only by several successive years of above-average annual rainfall. The importance of green grass during the dry season as a key resource is emphasized, not only for tsessebe, but also for other African antelopes that graze selectively. **Key words: antelope, precipitation, nutrition, mortality**

081

Eastman, D. S. 1978. Habitat selection and use in winter by moose in sub-boreal forests of north-central British Columbia, and relationships to forestry. PhD thesis, University of British Columbia, Vancouver, BC. Chapter 9 presents an analysis of the effects of forests on winter climate, largely snow (see Forest-Snow annotated bibliography); pages 370-378 discuss the relationship between snow depth

and forest canopy. The effect of snow on moose migration and habitat use is discussed. Moose shifted to forested habitat as snow depths approached critical levels. Snow density was usually of little importance although it may be of greater importance in low snowfall areas. Quamaniqs were extensively used by moose. Moose use of an apparently uniform forest type was nonrandom; they selected microsites. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver, BC, Canada, p. 22.) **Key words: moose, snow, migration, habitat use**

082

Edwards. R. Y. 1956. Snow depths and ungulate abundance in the mountains of western Canada. Journal of Wildlife Management 20(2):159-168. Abstract: There have been alternating periods of deep snow winters and shallow snow winters in British Columbia. Population declines in ungulates have occurred in deep snow periods. The record is most complete for mule and black-tailed deer and moose, but other species appear to have shown similar fluctuations. Annual reports from the Cassiar region from 1909 to 1919 shows that the Cassiar thinhorn sheep have followed the same trends as deer, moose, and perhaps caribou in this period.

Limited information from Alberta and Alaska indicates that the former has experienced similar weather and ungulate fluctuations, while the latter shows no conclusive agreement.

Ungulate declines in the past have been blamed on a long and varied list of supposed causes. Snow depths may be the primary cause of a number of factors observed in winter mortality of ungulates.

The seriousness of declines due to snow may vary with the ranges concerned. What appears to be over-use in deep snow years may involve only a small part of the range used at other times.

In British Columbia the record of ungulate fluctuations indicates that the human harvest is not a major population control, at least on the more common species.

As long as ungulate herds can increase rapidly from the effects of winters with deep snow, weather, not hunting, is the more important control over their numbers.

A different facet of the role of snow in ungulate management in mountainous terrain concerns human influences upon small areas of land essential for ungulate survival in winters with deep snow. These areas are usually on warm slopes at low elevations where most subject to the influence of man. Farming may result in range destruction, while livestock grazing, logging, fire and other influences may have equally drastic effects. Ungulate herds which populate large areas under favourable weather conditions may be exterminated if these small and only occasionally essential ranges are not available when needed. This appears to partly explain the disappearance of bighorn sheep from the rims of dry valleys in southern British Columbia. A number of mule deer herds have been similarly affected. This trend is difficult to combat because the situation is not easy to see. There may be long periods of years without sufficiently severe winters to make these areas essential for survival. As a result, destruction of emergency range may not seriously affect the ungulate population using it for many years. Public acquisition of small areas of low elevation winter range may be essential to ensure ungulate abundance over many square miles. **Key words: snow, bighorn, mule deer, moose, caribou, habitat use**

083

Egan, J. L. 1971. Mule Deer. Pages 53-69 *in* T. W. Mussehl and F. W. Howell, eds. Game Management in Montana. Montana Fish and Game Department, Helena, Montana. Notes: Egan notes that the drought of the 1930s played a great role in the decimation of mule deer in Montana and hence in the state's conservation movement. "The great drought of the 1930's resulted in much national and state conservation legislation. People in Montana voiced concern over declines in wildlife, including deer. Many preserves were established, hunting was curtailed and deer transplanting suggested. Between 1941-56, more than 1,300 mule deer were trapped and transplanted in the state. This program was designed to increase the lagging deer population of the 30's. Although many of the deer were not transplanted until around 1947-50, it is likely this postwar segment of the program only hastened along the natural deer increase that was already underway." (Due to increase in precipitation and habitat improvement.) **Key words: drought, precipitation, mule deer, conservation, legislation**

084

Egorov, O. V. 1967. Wild ungulates of Yakutia. Israel Program for scientific Translations, Jerusalem. Snow is the environmental factor exerting the greatest influence on wild ungulates of the Yakutia region of Siberia. Snow is loose in Yakutia and does not support even "snow-shoe" type ungulates (reindeer and musk deer). A large hoof surface is detrimental to animals with "silt" type legs since hooves only slightly submerged in the snow cannot give a sharp strike during flight. In this case, an increase in foot-loading facilitates rapid movement. "Dense snow which carries its weight is more favourable for animals with "snowshoe" hooves; such ungulates prefer loose but shallow snow [sic]." The length of the leg and the looseness or density of the snow are of primary importance. An index of ability to move through the snow ("index of passage") is formulated by dividing chest height (cm) by the product of snow depth (cm) and snow density (g/cm^2)[sic].Reduction of the index implies increased difficulty of movement until a critical region is reached when the snow is strong enough to support the animal. The critical snow density, at depths of chest height, are 0.18-0.20. The critical value for the index of passage is therefore about the same for all ungulates – about 5. The density needed to support an animal ranges from 0.20 in musk deer to 0.40 in wapiti. In Yakutia, snow depths are rarely greater than 30 cm whereas density in early spring is about 0.20. The index of passage therefore varies from 6.7 in musk deer to 16.7 in elk. Normal snow conditions are therefore no obstacle to wild ungulates. Single species accounts of snow relations are then provided for musk deer, wapiti, roe deer, elk (i.e., moose), reindeer, and bighorn sheep. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver, BC, Canada, pp 22-23.) **Key words: snow, index, wild sheep, elk**

085

Einarsen, A. S. 1948. The pronghorn antelope and its management. The Wildlife Management Institute, Washington D. C. Notes: When a whole area becomes snow-covered there is a gradual drift to the ridges, where vegetative stands are more exposed and the animals find food more readily and are safer from predatory animals which have

an advantage in deep snow. Antelope will be forced off their usual range by heavy snowfalls and are helpless in deep snow if chased by coyotes. Snow which will carry the weight of coyotes breaks through and lacerates the legs of antelope. It has been observed that few losses occur when mule deer wintering on over browsed areas are forced by snow upon adjacent sagebrush flats. This is probably because of the high food value of sage. **Key words: antelope, mule deer, snow, predation, nutrition**

086

Enk, T. A., H. D. Picton, and J. S. Williams. 2001. Factors limiting a bighorn sheep population in Montana following a dieoff. Northwest Science 75(3):280-291. Abstract: Conservation and management of bighorn sheep populations is complicated by the species' susceptibility to a multitude of pathogens and the long-term influence of disease upon population dynamics. Small, post-dieoff sheep herds are often unable to fully recover to pre-dieoff densities, and researchers have identified several factors limiting such populations including disease, predation, competition, climate, nutritional deficiencies, and loss of genetic variability. We studied a small bighorn sheep herd in west central Montana from 1995 to 1997 to identify the mechanisms responsible for poor population performance subsequent to a dieoff in 1984. In contrast to the migratory pre-dieoff population, the current sedentary population was restricted to a small area of low elevation range throughout the year. Whereas we observed limited annual adult mortality due to disease and predation, ewe productivity and lamb recruitment rates were low in all years. Lamb production and survival were highly correlated with summer climatic conditions, with the highest rate of disease-mediated lamb mortality occurring during a summer drought and the lowest rate of ewe productivity occurring subsequent to this drought. Our data suggest that disease continues to play a significant role in this bighorn sheep population, and nutritional quality of summer forage influenced not only sheep immunocompetence and susceptibility to disease but also herd productivity. Winter is generally considered the critical season for ungulate populations in the northern Rocky Mountains, yet summer climatic conditions can have important implications for performance of sedentary, low elevation sheep populations. We suggest that an understanding of population-specific limiting factors is essential to successful management of post-dieoff bighorn sheep herds. Data obtained through rigorous field studies facilitate the development and implementation of efficient, biologically sound strategies to improve performance of these populations. **Key words: wild sheep, mortality, drought, disease, nutrition, movement**

087

Epps, C. W. 2004. Population processes in a changing climate: extinction, dispersal, and metapopulation dynamics of desert bighorn sheep in California. Dissertation, University of California, Berkeley. Abstract: Metapopulations may be very sensitive to rapid global climate change. I compared existing and historical population distributions of desert bighorn sheep (*Ovis canadensis nelsoni*) in California and found that regional climate patterns were correlated with local population extinction. I used these relationships to model population vulnerability to extinction under current climatic conditions and future climate change. I collected diet samples in 18 mountain ranges to determine how climatic variation affected diet quality. Desert bighorn in lower-elevation populations had poorer diet quality. Diet quality during reproduction was

strongly and positively correlated with winter precipitation; the effect of increased temperature varied depending on the time of year. I used these relationships to evaluate how diet quality, and subsequently demography, of desert bighorn sheep will be affected by predicted changes in climate in the coming century. To understand how colonization and dispersal between these populations might off-set population extinction, I collected and analyzed fecal DNA from 406 desert bighorn in 29 populations. I used microsatellite loci and mitochondrial DNA sequences to assess gene flow across human-made barriers and determine the geographic scale of dispersal. I documented a recent and rapid reduction in genetic diversity due to only 40 years of anthropogenic isolation: interstate highways, freeways, canals, and developed areas, where present, have apparently eliminated gene flow. Populations exhibit strong spatial structure with little gene flow occurring over inter-population distances by 15 km. Finally, I tested whether genetic diversity was lower in populations predicted to be at high risk of climate-related extinction, after controlling for population connectivity. I found that populations predicted to be at high risk of climate-related extinction had lower allelic richness and heterozygosity, suggesting history of smaller effective population sizes and more bottlenecks. I argue that connectivity must be maintained to help offset loss of populations and genetic diversity resulting from global climate change. While it is not clear whether the numerous population extinctions in the last century result from climatic variation or climate change, it is clear that increased aridity and anthropogenic habitat fragmentation will jeopardize the persistence of many of the remaining populations of desert bighorn sheep in California. **Key words: wild sheep, precipitation, genetics, model**

088

_____, P. J. Palsbøll, J. D. Wehausen, G. K. Roderick, and D. R. McCullough. 2006. Elevation and connectivity define genetic refugia for mountain sheep as climate warms. Molecular Ecology 15:4295-4302. Abstract: Global warming is predicted to affect the evolutionary potential of natural populations. We assessed genetic diversity of 25 populations of desert bighorn sheep (*Ovis canadensis nelsoni*) in southeastern California, where temperatures have increased and precipitation has decreased during the 20th century. Populations in low-elevation habitats had lower genetic diversity, presumably reflecting more fluctuations in population sizes and founder effects. Higher-elevation habitats acted as reservoirs of genetic diversity. However, genetic diversity was also affected by population connectivity, which has been disrupted by human development. Restoring population connectivity may be necessary to buffer the effects of climate change on this desert-adapted ungulate. **Key words: wild sheep, genetics, temperature, precipitation**

089

_____, D. R. McCullough, J. D. Wehausen, V. C. Bleich, and J. L. Rechel. 2004. Effects of climate change on population persistence of desert-dwelling mountain sheep in California. Conservation Biology 18(1):102-113. Abstract: Metapopulations may be very sensitive to global climate change, particularly if temperature and precipitation change rapidly. We present an analysis of the role of climate and other factors in determining metapopulation structure based on presence and absence data. We compared existing and historical population distributions of desert bighorn sheep

(*Ovis canadensis*) to determine whether regional climate patterns were correlated with local extinction. To examine all mountain ranges known to hold or to have held desert bighorn populations in California and score for variables describing climate, metapopulation dynamics, human impacts, and other environmental factors, we used a geographic information system (GIS) and paper maps. We used logistic regression and hierarchical partitioning to assess the relationship among these variables and the current status of each population (extinct or extant). Parameters related to climate—elevation, precipitation, and presence of dependable springs—were strongly correlated with population persistence in the twentieth century. Populations inhabiting lower, drier mountain ranges were more likely to go extinct. The presence of domestic sheep grazing allotments was negatively correlated with population persistence. We used conditional extinction probabilities generated by the logistic-regression model to rank native, naturally recolonized, and reintroduced populations by vulnerability to extinction under several climate-change scenarios. Thus risk of extinction in metapopulations can be evaluated for global-climate-change scenarios even when few demographic data are available. **Key words: wild sheep, extinction, genetics, model, precipitation**

090

Ericsson, G., J. P. Ball, and K. Danell. 2002. Body mass of moose calves along an altitudinal gradient. Journal of Wildlife Management 66(1):91-97. Abstract: We tested whether altitude increased environmental heterogeneity in moose (*Alces alces*) populations on the landscape scale. Dressed mass from moose calves collected during 10 consecutive years was related to local climate information from 26 different weather stations (located from 7 to 525 m above sea level). Two hypotheses were contrasted: (l) Are moose offspring from higher altitudes heavier because of increased forage quality with increasing altitude? Or (2) Are moose offspring from lower altitudes heavier because the growing season is longer there so that the time moose calves can grow is extended at these lower altitudes? During October (when moose calves stop growing), both sexes showed a significant negative relationship with altitude. The dressed body mass of female calves was more affected by increased altitude (-1.4 kg per l00 m increase in altitude) than males (-0.8 kg per 100 m). The mass of both sexes was positively related to the length of the growing season (i.e., days >6°C). Female mass showed significant cohort effects during 4 of the 10 years investigated (range -6.3 to 3.4 kg), whereas males showed cohort effects during 2 years (-3.7 to 3.5 kg). We conclude that the annual variation in the length of the growing season together with year-specific effects may introduce considerable spatial and temporal variation in moose population dynamics mediated via offspring body mass. We suggest that this impact on population dynamics may be most pronounced at higher altitudes. Our analysis further suggests that a permanent factor (altitude) may interact with random variations (weather) to influence the length of the growing season and thus complicate the management of moose populations by creating cohorts composed of females of unequal quality. We suggest that managers be alert for sudden changes in ungulate recruitment due to unusually weak or strong cohorts reaching reproductive age. **Key words: moose, population dynamics, nutrition**

091

Farnes, P. E. 1996. An index of winter severity for elk. U. S. Department of Interior Technical Report NPS/NRYELL/NRTR/96-01. Abstract: A simple procedure for indexing the severity of winters for wildlife would help wildlife managers and the public assess the relative severity of any given winter and its effect on wildlife. The index of winter severity has a scale from -4 for the most severe winter to +4 for the mildest winter; 0 represents an average winter. The index incorporates the minimum daily temperatures below a threshold level (wherein basal metabolic rate increases with colder air temperatures), the snow water equivalent (the amount of water contained in the snow pack) that impedes animal movement and increases the effort required to obtain forage), and the precipitation during the previous summer that determines forage production. Long-term weather station and snow course data on the winter range were used to represent conditions on the lower northern winter range. Statistical procedures were used to determine probability levels for the different variables. The values from the 1 to 99% probabilities were converted to the -4 to +4 scale. The index of winter severity for elk (*Cervus elaphus*) for the lower northern winter range in and north of Yellowstone National Park was calculated for 1949 through 1993. Index of winter severity and the northern elk herd recruitment rate is compared for 1974 through 1992. There is some relation between index of winter severity and hunter harvest outside the park and between index of winter severity and recent elk population. **Key words: elk, temperature, snow, precipitation, index**

092

_____. 1991. A scaled index of winter severity. Western Snow Conference 59:[pages not given]. Summary: Farnes describes an index of winter severity. The IWS provides wildlife managers and the public with an easily understood numeric measure of how mild or severe any period or winter, or series of winters, may be or have been. It provides a method for combining different variables such as temperature, snow, and precipitation into a single index. It also enables indexes to be calculated for different areas and to be tailored to different species of animals. As more experience is gained with the IWS, the procedures for determining the weightings of each variable for each species should become more scientific and effects of winter severity on populations should become more evident. **Key words: index, temperature, snow, precipitation**

093

_____, C. Heydon, and K. Hansen. 2000. Climate data collection, computation and analysis for population ecology of white-tailed deer in northwest Montana. Project W-100-R-4 Final Report, Montana Department of Fish, Wildlife and Parks, Helena. Introduction: This study's objective is to process historic data on snowpack distribution in and adjacent to the Bowser/Tally Lakes and Murphy/Dickey Lake white-tailed deer (*Odocoileus virginianus*) summer and winter range areas in northwest Montana. In addition to snow data, daily precipitation and temperature data were processed for correlation with soil moisture, forage production, plant phenology, and other plant/soil moisture/animal relationships. Variability in other natural processes, such as recovery from logging, insects and fires or lack of fires, may also be correlated to variations in snow, precipitation, and/or temperature.

An Index of Winter Severity (IWS) based on snow, temperature and forage parameters was calculated for two winter ranges. The IWS relates to physical condition and mortality of ungulates which in turn relates to population dynamics. The physical condition of ungulates in winter and early spring may also relate to predation. A summary of data for stations in and near the study area is included. **Key words: white-tailed deer, index, snow, precipitation, temperature, population dynamics, predation**

094

_____, C. L. Heydon, and K. J. Hansen. 1998. Using climatic data to develop an index of winter severity and responses by large mammals. Intermountain Journal of Sciences 4(3/4):92. Abstract (only): Daily climatic data are obtained by Natural Resources and Conservation Service (NRCS), SNOTEL stations and National Weather Service (NWS), and climatological (CLIM) stations. SNOTEL sites are usually in mountain locations in western US and provide near-real-time, year around, daily data on snow water equivalent (SWE), precipitation, maximum, minimum and average air temperatures (TMAX, TMIN, TAVG). CLIM sites are usually at valley locations and provide daily precipitation, TMAX, TMIN, TAVG and snow depth (SNWD). After all missing data are estimated by correlation with nearby sites, daily SWE and snow density are estimated at CLIM sites using precipitation, SNWD and TAVG. The Keetch/Byram drought index (KBDI), a soil moisture deficit model, and accumulated growing degree days are also computed. The Index of Winter Severity (IWS) for each winter range is calculated using SWE for the snow index, minimum temperatures below the effective critical temperature for each species for temperature index, and KBDI and growing degree-days for the winter forage index. The snow, temperature and forage indexes are weighted and combined to provide an IWS on a scale from +4 for the mildest of historic conditions to -4 for the most severe conditions. The IWS is one of the factors relating to mortality, reproduction and predation of big game animals. Accumulation of SWE on summer and transitional ranges is related to migration to winter ranges. Winter temperature, forage and SWE are related to declines in fat reserves and winter mortality. **Key words: index, snow, temperature, precipitation**

095

Feder, C., M. Festa-Bianchet, C. Bérubé, and J. Jorgenson. 2007. Effects of birth date, sex, maternal characteristics, and environmental conditions on mass and survival of bighorn lambs. Biennial Symposium Northern Wild Sheep and Goat Conference 15:56. Abstract (only): For ungulates living in strongly seasonal environments, variation in parturition date should have strong fitness consequences. We investigated birth date interactions with sex, maternal characteristics, and environmental variables to affect the growth and survival of bighorn sheep (*Ovis canadensis*) lambs and yearlings. Over 13 yr, the estimated birth date of 206 lambs ranged from May 21 to July 18. Late-born lambs of both sexes were lighter at weaning than early-born lambs. Weaning success of the mother the previous year and November to December precipitation affected the date of birth. Birth date had no effect on lamb summer growth rate. To assess the parameters affecting lamb mass at weaning, we tested a model including lamb characteristics, maternal previous reproductive status, maternal mass and age, and environmental conditions. Fecal crude protein values during summer

correlated positively with lamb mass in September. Birth date affected lamb survival if considered alone, but not when weaning mass was included in the model. Birth date had a negative effect on yearling mass in early June. However, when accounting for the mass of lambs in September, birth date was not significant on mass of yearlings and 2-yr-olds in June and September for either sex. Lamb mass in September correlated with June and September mass as yearlings, but had no correlation with mass at 2 yr. Our results suggest that birth date affects several traits of individuals, such as mass in June and September. This, in turn, affects survival and ultimately may affect individual fitness. During the short growing season, bighorn lambs must accumulate sufficient body resources to survive winter, and females may be selected to synchronize birth with forage productivity. Our data also suggest complex relationships among different factors, the maternal quality plays an important role in affecting lamb life history. **Key words: wild sheep, precipitation, parturition, model**

096

Feldhamer, G. A., T. P. Kilbane, and D. W. Sharp. 1989. Cumulative effect of winter on acorn yield and deer body weight. Journal of Wildlife Management 53(2):292-295. Abstract: We examined the effects of cumulative winter climate on acorn yield and body weight of immature white-tailed deer (*Odocoileus virginianus*) the following autumn, and spring population density of deer on Land Between the Lakes (LBL), Tennessee. Body weights of male and female fawns and yearlings were positively correlated with acorn yield the previous autumn and inversely correlated with estimated spring population density of deer. Acorn yield was positively related, and spring population density of deer inversely related, with the cumulative number of days with >0.25 cm of precipitation during the previous 3 and 4 winters. Acorn yield and associated body weights were not related to total amount of precipitation, presumably because of the topography of the study area. Cumulative effects of winter climate should be considered in deer population models. **Key words: white-tailed deer, precipitation, nutrition**

097

Ferrari, M. J. and R. A. Garrott. 2002. Bison and elk: brucellosis seroprevalence on a shared winter range. Journal of Wildlife Management 66(4):1246-1254. Abstract: An increase in the population of Yellowstone bison (*Bison bison*) and changes in their winter distribution have prompted concerns about the potential for bison to transmit brucellosis to cattle. Elk (*Cervus elaphus*) are also hosts for the disease organism and could play a role as reservoirs for the disease. Environmental conditions on the Madison-Firehole winter range promote a high degree of range overlap between bison and elk (53% in Dec to 76% in May). Radiocollared elk were located within 100 m of bison 18% of the time, and commingling between species was positively correlated with snowpack. We investigated the seroprevalence of elk of the Madison-Firehole winter range and made comparisons to other elk populations in the region as an indicator of potential for interspecies transmission of brucellosis in the wild. We found that the seroprevalence rate in the Madison-Firehole elk (3%; n = 73) was consistent with elk that do not commingle with bison (0-1%) and lower than in elk associated with supplemental feeding programs (25-37%). Despite high levels of commingling, the seroprevalence rate in the Madison elk herd suggests that interspecies transmission from bison to elk in the Madison-Firehole is low. **Key words: bison, elk, snow, disease**

098

Flueck, W. T. 2001. Offspring sex ratio of introduced red deer in Patagonia, Argentina after an intensive drought. Journal of Neotropical Mammalogy. 8(2):139-147. Abstract: Red deer (*Cervus elaphus*) introduced to Patagonia have reached high densities in the forest-steppe ecotone. Drought conditions during 1998/99 were suspected to impact subsequent reproductive performance. Necropsies of 50 adult females during the 1999 winter revealed lowered pregnancy rates and lactation in 32% of non-pregnant as opposed to 0% among pregnant females. There were no signs of fetal resorptions or abortions. The fetal sex ratio (20m:8f) deviates significantly from unity, and mothers with female or male fetuses averaged 6.7 and 5.2 years, respectively (P = 0.14). However, 90% of primiparous females (2.5 years old) had males, the following age class had all females, the middle age class (5-8 years old) had all males, and older females had equally male or female fetuses. These females were at borderline of body condition allowing conception and thus were at extremely low levels of condition during breeding. The male-biased fetal sex ratio contrasts reports of other studies that only females in best condition tend to have male-biased offspring. However, ambivalent results from other studies may stem from not having evaluated body fat reserves and reproductive tracts, or studies done during environmental conditions not extreme enough. The present results also indicate that red deer populations occur at densities where they can easily become food-limited through a singular environmental phenomenon such as a drought. Although recruitment rates would be drastically reduced through such temporary food shortage, red deer will recuperate rapidly and will continue to exert intensive pressure on the flora causing subsequent damage if population densities are not lowered through hunting. **Key words: red deer, drought, sex ratio, nutrition**

099

Forchhammer, M. C., T. H. Clutton-Brock, J. Lindstrőm, and S. D. Albon. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. Journal of Animal Ecology 70:721-729. Summary: 1. Density-dependent and climatic conditions experienced by individuals before and after birth differ considerably between cohorts. Such early environmental variability has the potential to create persistent fitness differences among cohorts. Here we test the hypothesis that conditions experienced by individuals in their early development will have long-term effects on their life history traits. 2. We approached this by analyzing and contrasting the effects of climate (the North Atlantic Oscillation, NAO) and population density at year of birth on cohort birth weight, birth date, litter size, age of maturity, survival and fecundity of Soay sheep, *Ovis aries* L., ewes in the population of Hirta, St Kilda, Scotland. 3. Significant intercohort variations were found in life history traits. Cohorts born after warm, wet and windy (high NAO) winters were lighter at birth, born earlier, less likely to have a twin and matured later than cohorts born following cold and dry (low NAO) winters. High population densities in the winter preceding birth also had a negative effect on birth weight, birth date and litter size, whereas high postnatal densities delayed age of first reproduction. 4. High NAO winters preceding birth depressed juvenile survival but increased adult survival and fecundity. The negative influence of high NAO winters on juvenile survival is likely to be related to mothers' compromised physical condition while the cohort is *in utero*, whereas the positive influence on adult survival and fecundity may

relate to the improved postnatal forage conditions following high NAO winters. High pre- and postnatal population densities decreased juvenile (neonatal, yearling) and adult (2-4 years) survivorship but had no significant effect on fecundity. **Key words: density, Soay sheep, fecundity, nutrition, NAO, precipitation**

100

_____, N. Chr. Stenseth, E. Post, and R. Langvatn. 1998. Population dynamics of Norwegian red deer: density-dependence and climatic variation. Proceedings of the Royal Society of London B 265:341-350. Abstract: We present a model on plant-deer-climate interactions developed for improving our understanding of the temporal dynamics of deer abundance and, in particular, how intrinsic (density-dependent) and extrinsic (plants, climate) factors influence these dynamics. The model was tested statistically by analyzing the dynamics of five Norwegian red deer populations between 1964 and 1993. Direct and delayed density-dependence significantly influenced the development of the populations: delayed density-dependence primarily operated through female density, whereas direct density-dependence acted through both female and male densities. Furthermore, population dynamics of Norwegian red deer were significantly affected by climate (as measured by the global weather phenomenon, the North Atlantic Oscillation: NAO). Warm, snowy winters (high NAO) were associated with decreased deer abundance, whereas the delayed (two-year) effect of warm, snowy winters had a positive effect on deer abundance. Our analyses are argued to have profound implications for the general understanding of climate change and terrestrial ecosystem functioning. **Key words: NAO, red deer, population dynamics, model**

101

_____ and D. Boertmann. 1993. The muskoxen *Ovibos moschatus* in north and northeast Greenland: Population trends and the influence of abiotic parameters on population dynamics. Ecography 16(4):299-308. Abstract: This paper presents the first long term (1960-89) data set on both muskox *Ovibos moschatus* density and weather patterns in north and northeast Greenland. The muskoxen appear to have experienced a 25-year favorable period from the early 1960s to the mid 1980s, in which density increased and reached a maximum level. The population minimum around 1960 probably represents a long term minimum, following a long, generally unfavorable period between 1940-60. Variation in the local population trends from the southern parts of the muskox distribution in northeast Greenland to the northern parts, can be divided into three geographical areas where density dependent and density independent factors affecting muskox populations are apparently different. Regional population stability does not increase towards the north. Two density independent (abiotic) factors seem to be of prime importance in determining the muskox population density and distribution in northeast Greenland: i) the amount of winter precipitation affects the distribution of muskoxen negatively, inducing local migrations, but does not have a direct negative effect on large scale variation in density; ii) ablation (i.e. melting of the upper snow layer) and concomitant ice crust formation in winter have a highly negative effect on muskox density in the southern range, but not in the northern range. The two abiotic factors, which show a considerable variation from north to south, are statistically independent and seem to be triggered by different weather conditions. The predictions that follow from a climatic model both with respect to the direct influence of abiotic factors on

muskox density and the indirect influence of climatic fluctuation are not fully supported by the data presented here. **Key words: muskoxen, precipitation, snow, ice, density, temperature, movement**

102

Formozov, A. N. 1946. Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds. Translated and published by the Boreal Institute, University of Alberta, Edmonton, Alberta, Canada. Occasional Paper No. 1. A synthesis of the author's life-long preoccupation with snow. The chapter titled "Snow in Forest Regions" gives Siberian hunter terminology for snow-types, describes lesser accumulations (by 2-3 times) under the forest canopy, snow compaction in the forest, differential snowmelt rates under canopies and in the open and reviews the early Soviet literature. The chapter titled "Snow Cover as an Obstacle Hindering the Movement of Animals" is largely descriptive and anecdotal; some foot-loadings are given. The influential distinction is made between "chionophobes", "chionophores" and "chionophiles". Snow as a factor influencing migration and snow-related winter mortality is discussed. An extensive treatment is given of the manner in which snow influences the distribution and migration of Soviet mammals and birds. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver, BC, Canada, p.23.) **Key words: snow, mortality, distribution, movement**

103

Forrester, D. J. and R. C. Littell. 1976. Influence of rainfall on lungworm infections in bighorn sheep. Journal of Wildlife Diseases 12:48-51. Abstract: From 1959 through 1968, lungs from 124 Rocky Mountain bighorn sheep (*Ovis c. canadensis*) from the Sun River herd in western Montana were examined for lungworm infections. All lungs were infected with *Protostrongylus stilesi* and 104 (84%) contained concurrent infections of *P. stilesi* and *P. rushi*. Significant correlations were observed between levels of lungworm infection and total rainfall during April, May, and June for each year. An explanation of this in terms of terrestrial snail (intermediate host) populations and a suggestion for the possible use of these data in developing a predictive model for forecasting lungworm levels for use in bighorn sheep management are given. It may be desirable to increase harvest levels of bighorn sheep in years of abnormally high amounts of rainfall during April, May, and June to insure the safe overwintering of a smaller but healthier herd of bighorn sheep rather than risk the chance of increased winterkills due to high lungworm infections and their contribution to the bighorn sheep pneumonia complex. Other interacting factors or combinations of factors in addition to rainfall (e.g. temperature, relative humidity, etc.) may prove useful in refining such a predictive model, increasing its value for management of bighorn sheep. **Key words: wild sheep, precipitation, disease, temperature**

104

Frank, D. A. and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73(6):2043-2058. Abstract: The purpose of this study was to examine the effect of abundant native large

herbivores on ecosystem function of a spatially and temporally heterogeneous temperate grassland. Net aboveground primary production (ANPP), large herbivore consumption (C), and dung deposition (D), an index of nutrient flow from herbivores to the soil, were measured in grassland and shrub-grassland habitat on winter, transitional, and summer range used by herds of elk (*Cervus elaphus*) and bison (*Bison bison*) in northern Yellowstone National Park. Temporary exclosures (5-7 per site) were moved every 4 weeks during the snow-free season to determine ANPP and C. Data were collected during 1988, a year of drought and unusually high elk and bison population levels, and 1989, a climatically near-average year, with dramatically fewer elk and bison.

All three processes, ANPP, C, and D, varied widely among sites: ANPP range: 16-589 g/m^2, C range: 0-306 g/m^2, and D range: 0-68 g/m^2. An average of 45% of ANPP was consumed by herbivores. Production and consumption, and consumption and dung deposition were positively correlated across all sites. In addition, sites were grazed when plants were growing.

There was a 19% reduction in ANPP from 1988 to 1989, likely caused by death or injury to plants during the 1988 drought. Drought also appeared to be partially responsible for reductions in elk and bison from 1988 to 1989, which were coincident with declines in C and D. Results indicate direct effects and suggest indirect effects of a single-season drought on grassland function that will persist for several years after the event. **Key words: elk, bison, drought, forage quality, migration**

105

Frisina, M. R., O. Yondon, and R. M. Frisina. 2007. Population status of Mongolian argali (*Ovis ammon*) with reference to sustainable use management. Journal of the Bombay Natural History Society 104(2):142-146. Summary: The authors note that a low lamb:ewe ratio in Mongolian argali was likely related to severe winter conditions (deep snow and low temperatures) the previous year followed by a severe drought. These weather conditions persisted from 2000-2002 and occurred for a 3-year period prior to the population survey reported. Due to the depressed lamb:ewe ratio, the lower proportion of rams in 2002 was likely a result of winter mortality during recurrent severe winters from 1991-2002. **Key words: wild sheep, drought, snow, temperature**

106

_____and K. S. Douglass. 1990. Diastema Length as an indicator of skeletal development in Rocky Mountain Elk (*Cervus elaphus*). Proceedings of the Montana Academy of Sciences 50: 9-11. Abstract: Correlation between diastema length and age in female Rocky Mountain elk (*Cervus elaphus*) were studied to determine if diastema length is a reliable indicator of skeletal development. A significant statistical relationship was found for age groups 5 years through 3.5 years; age classes 4.5 years and older evidenced no significant statistical relationship. The data indicate female elk skeletons are essentially developed at 4.5 years and that diastema lengths of elk in the .5 and 1.5 year age groups probably serve as the most sensitive indicator of changes in population condition. **Key words: index, elk, nutrition**

107

_____ and _____. 1989. Using diastema length as an indicator of body condition in fawn and yearling mule deer. Proceedings of the Montana Academy of Sciences 49:23-26. Abstract: Diastema lengths measured in fawn and yearling mule deer were positively correlated to changes in body weight that occurred when comparing wet and dry growing seasons. Diastema lengths of fawn and yearling male mule deer were found to be a valid index for monitoring changes in population condition. The study was conducted in southwestern Montana by Department of Fish, Wildlife and Parks. **Key words: index, mule deer, precipitation**

108

Fuller, J. A. 2006. Population demography of the Yellowstone National Park bison herds. Thesis, Montana State University, Bozeman, USA. Summary: The bison population of Yellowstone National Park (YNP) represents an outstanding conservation success story, as their numbers have increased from just 46 in 1902 to >4,000 today. Bison are keystone herbivores in YNP, and are central to several management controversies due to their infection with brucellosis. I integrated 100 years of historical count data with 7 years of recent vital rate data, and parameterized a matrix model using these vital rates to validate population growth estimates and to project future management scenarios involving disease control through vaccination and/or culling programs. From count data, I determined that historical population growth rates were heavily influenced by supplemental feeding, resulting in high population growth rates (ƛ=1.17). I found evidence for density dependence in two subpopulations, the northern and central herds. The herds displayed divergent population dynamics over 1970-1981 and 1982-2000, as density dependence weakened in the northern herd and increased in the central herd, and herd growth rates were negatively correlated after 1982 (R^2=0.40, P<0.01). I postulate the severe winter of 1982 catalyzed emigration from the central herd to the northern herd. Survival and birth rates did not differ between the herds 1995-2001, and calf-adult ratios did not differ between the herds or the periods. I found that snow pack was negatively associated with the central herd population growth rates, and with spring calf ratios and recruitment (R^2=0.26-0.60, P<0.05). Birth rates were not variable with density-dependent or density-independent factors, but did vary according to serological status for brucellosis and with age structure, as primiparous bison had lower birth rates than adults. I did not detect reproductive or survival senescence. Adult survival rates were high and static (0.92). Integrating these vital rates into a matrix model resulted in a population growth rate estimate of ƛ=1.07, which closely corroborated an estimate of ƛ from count data during 1990-2000 (ƛ=1.05). Simulating the effects of brucellosis eradication through vaccination programs resulted in ƛ=1.09, roughly a 29% increase. I concluded brucellosis eradication could further increase bison population growth rates, exacerbating conflicts outside YNP. **Key words: bison, snow population dynamics, disease**

109

Fuller, T. K. 1991. Effect of snow depth on wolf activity and prey selection in north central Minnesota. Canadian Journal of Zoology 69:283-287. Abstract: Wolf (*Canis lupus*) activity and interactions with white-tailed deer (*Odocoileus virginianus*) were

monitored in north central Minnesota during six winters in which mean January-February snow depth alternated between shallow (19-26 cm) and relatively deep (40-47 cm) and winters (winter severity index; L. J. Verme. 1968. J. Wildl. Mnage. 32:566-574) alternated between mild (71-98) and moderately severe (126-137). Wolves traveled farther and more often and spent less time with other pack members in mild than in severe winters. Radio-marked wolves and deer used conifer cover less, and fewer deer were killed there, when snow was shallow. Similarly, fewer wolf-killed deer were found in and near deer concentration areas during mild winters. Of the 74 deer killed by wolves, the proportion that were fawns (54%) differed from the proportion of fawns in the winter population (27%), but neither varied with winter severity. Few deer killed by wolves appeared debilitated. Carcass consumption was high in all winters, regardless of their severity, but wolves scavenged less in mild than in severe winters (10 vs. 29% of deer carcasses observed). Thus, wolves changed winter activity, movement patterns, sociality, and feeding behavior in response to snow-induced changes in deer distribution and mobility. **Key words: white-tailed deer, snow, predation**

110

Gaffney, W. S. 1941. The effects of winter elk browsing, South Fork of the Flathead River, Montana. Journal of Wildlife Management 5(4):427-453. Abstract: The amount of snow that elk can negotiate depends on vegetation characteristics, snow characteristics, age and condition of the animals, and topography. Soft snow depths of 30 inches caused elk to shift to browse. Browse plants are raised above the ground and are more available even when buried. Hardpacked snow, 12-24 inches deep, may be sufficient to cause a shift to browse. Mature elk moved with difficulty through loose snow 40 inches deep or crusted snow 30 inches deep. The maximum depth elk could tolerate was generally about 48 inches. Calves and weakened adults could not negotiate snow deeper than 30 inches. Topography became an influence when snow depths reached 30 inches. Elk tolerated 12-18 inches more snow on the flats than on a hillside. (Annotation by Shank and Bunnell 1982: *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver BC Canada, pp 23-24.) **Key Words: elk, snow, movement, nutrition**

111

Gaillard, J-M, P. Duncan, D. Delorme, E. Van Laere, N. Pettorelli, D. Maillard, and G. Renaud. 2003. Effects of hurricane Lothar on the population dynamics of European roe deer. Journal of Wildlife Management 67(4):767-773. Abstract: Although extreme weather events—such as hurricanes—cause obvious changes in landscape and tree cover, the impact of such events on population dynamics of ungulates has not yet been measured accurately. We report a first quantification of the demographic consequences on roe deer (*Capreolus capreolus*) of the strongest hurricane (Lothar) that France has suffered in centuries. Based on long-term monitoring (>20 yr) of known-age individuals in 2 populations, we found that Lothar had no detectable negative effect on age- and sex-specific survival rates, except perhaps for old females. Likewise, although Lothar occurred during the time in the roe deer reproductive cycle when embryos are implanted, we found no evidence of a decrease in either the pregnancy rate or litter size. Our results show that roe deer populations are resistant to this kind of extreme weather event. The consequences for wildlife management are

direct and important: (1) the hunting bag was low in 2000 due to restricted hunter access, and (2) the main effect of hurricane Lothar was to create openings within large forests that are good habitat for roe deer. We suggest that Lothar will paradoxally have a positive effect on roe deer population dynamics. **Key words: roe deer, wind, population dynamics, habitat use**

112

Garel, M., A. Loison, J.-M. Gaillard, J.-M. Cugnasse, and D. Maillard. 2004. The effects of a severe drought on mouflon lamb survival. Proceedings of the Royal Society of London B 271:S471-S473. Abstract: The mouflon population of Caroux-Espinouse, southern France, inhabits a highly seasonal area with dry summers. We monitored summer lamb survival during a severe drought in 2003, from early June to late August. The survival of 35 radio-tagged lambs over nine two-week periods was strongly affected by the timing of rainfall. Survival depended on the amount of rainfall recorded at a given 14 day period and in the previous 14-21 day period. Survival was not influenced by the exceptionally high mean daily temperature recorded during some periods. Male lamb survival (0.68) tended to be less than female survival (0.81), although not significantly, possibly because of a low sample size. The high lamb mortality (25.7%) recorded during a four-month period is much higher than previous estimates of first-year mortality (less than 10%). We recommend accounting for climatic variation in summer when studying the population dynamics of ungulates. **Key words: wild sheep, drought, precipitation, mortality**

113

Garrott, R. A., L. L. Eberhardt, P. J. White, and J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. Canadian Journal of Zoology 81(1):33-45. Abstract: Variation in vital rates of an unharvested elk (*Cervus elaphus*) population was studied using telemetry for 7 consecutive years, 1991-1998. We found pronounced senescence in survival rates, but no evidence for reproductive senescence. Prime-age females (<10 years old) experienced very high annual survival rates (mean = 0.97, SE = 0.02), with lower survival rates for senescent animals ($\geq$10 years old; mean = 0.79, SE = 0.06). There was evidence that the severity of snowpack conditions had little effect on survival of prime-age animals except during the most extreme winter, while survival of senescent animals was progressively depressed as the severity of snowpack conditions increased. Reproductive rates remained essentially constant, near their biological maxima (mean = 0.91, SE = 0.02). Annual recruitment was highly variable. Snowpack had a pronounced effect on recruitment (r^2 = 0.91), the most severe snowpack conditions resulting in the virtual elimination of a juvenile cohort. Population estimates and recruitment rates obtained during this investigation and historic data collected from 1965 to 1980 support the premise that the population has been maintained in a dynamic equilibrium for at least three decades despite the stochastic effects of climate variation on vital rates. We conclude that the population is resource-limited, with variation about the equilibrium caused primarily by variable recruitment driven by stochastic annual snowpack. **Key words: elk, snow, recruitment, nutrition**

114

Garroway, C. J. and H. G. Broders. 2007. Adjustment of reproductive investment and offspring sex ratio in white-tailed deer (*Odocoileus virginianus*) in relation to winter severity. Journal of Mammalogy 88(5):1305-1311. Abstract: Both density-dependent factors and environmental stochasticity can impact the dynamics of free-ranging populations. The pathways through which these factors influence population dynamics can be complex and may be immediate or lagged, and cumulative effects of environmental factors have been reported. We examined the effects of the severity (snow depth and persistence and winter rainfall) of the current and previous winters on the probability that female *Odocoileus virginianus* adult and yearling white-tailed deer would produce a fetus, and that adult females would produce a male fetus. We used logistic regression and Akaike's information criterion to select the best models from a set of 11 *a priori* candidate models. The severity of the winter 1 year before gestation negatively impacted the probability that both adults and yearlings would produce a fetus. There was no evidence that the probability of yearlings or adults producing a fetus was affected by winter conditions while gestating. Further, there was no evidence that the severity of the winter during which a yearling was gestated affected its probability of producing a fetus as a yearling. As the severity of the winter of gestation increased, the probability of producing a male decreased, consistent with both the Trivers-Willard sex ratio adjustment hypothesis and the extrinsic modification hypothesis. We suggest that both the decreased probability of reproduction after severe winters and the variation in fetal sex ratio may ultimately increase lifetime fitness if they lead to the production of the fittest offspring given the available maternal resources. **Key words: white-tailed deer, sex ratio, snow, fecundity, population dynamics**

115

_____ and _____. 2005. The quantitative effects of population density and winter weather on the body condition of white-tailed deer (*Ocodoileus virginianus*) in Nova Scotia, Canada. Canadian Journal of Zoology 83:1246-1256. Abstract: Understanding the underlying mechanisms that cause variation in survival and the reproductive success of animals is essential for predicting variation in population parameters. To gain an understanding of the effects of density and winter weather severity on white-tailed deer, *Odocoileus virginianus* (Zimmermann, 1780), we examined the effects of current-year deer density and cumulative weekly average values for snow depth, rainfall, and the number of degrees below -15°C until the time of death, as well as cumulative effects of density and snow depth over the previous one and two winters, on the body condition of adult females, adult males, and fawns. Model selection using Akaike's Information Criterion and multi-model inference suggested that snow depth was the best predictor of body condition for all three age/sex groups. Winter rainfall was the next most influential predictor for adult females and adult males but was not important in determining fawn body condition. Temperature had the least influence on the body condition of all three age/sex groups. Deer density during the winter of death had minimal effects for all groups and we found no evidence that cumulative multiyear variables influenced body condition. We hypothesize that cohort variation may better explain previous findings showing effects of multiyear variables. A model for estimating the proportion of animals in poor body condition for each age/sex group is presented. **Key words: white-tailed deer, mortality, temperature, snow, model**

116

Gasaway, W. C., S. D. DuBois, S. J. Harbo, and D. G. Kelleyhouse. 1978. Preliminary report on accuracy of aerial moose surveys. Proceedings North American Moose Conference and Workshop 14:32-55. Abstract: Sample quadrats were established around radiocollared moose and each quadrat was surveyed with a search intensity of approximately 4 to 5 min/mi^2 using transect/contour searches similar to standard Alaska Department of Fish and Game surveys. A second, more intensive search of 10 to 13 min/mi^2 was then made of each quadrat. Substantially more moose were seen during the intensive search than during transect/contour surveys in all three physiographic areas. Habitat selected by moose was the most critical environmental factor affecting sightability of 45 radiotagged moose. During early and late winter, 84 and 61 percent, respectively of the radiocollared moose selected habitat types with low canopies (herbaceous, low shrub, and tall shrub). Moose utilizing these open habitats were easier to see regardless of search intensity. Moose using forest habitats were often missed during the initial transect/contour survey but were usually seen later during the intensive search. Spruce-dominated quadrats were the only areas in which uniformly high sightability could not be achieved with intensive search effort. Activity of moose also affected sightability. Lying moose were missed more frequently than standing moose during transect/contour surveys and intensive searches. Snow condition was identified as having considerable influence upon sightability, but the adverse effects of poor snow condition were largely overcome by intensive search effort. The application of these data to moose trend surveys and censuses is discussed. **Key words: moose, snow, census, habitat use, behavior**

117

Gates, C. C. and R. J. Hudson. 1979. Effects of posture and activity on metabolic responses of wapiti to cold. Journal of Wildlife Management 43(2):564-567. Summary: The authors studied the ecological bioenergetics of elk. In a cold environment metabolic rates of elk exhibited marked thermoregulatory responses to activity, likely via reduced insulation through increased convection, surface area, evaporation, blood circulation and changes in blood distribution. Activity in the cold resulted in a thermoregulatory penalty which increased in magnitude with level of activity. There is an energetic advantage of restricted activity in elk exposed to cold temperatures. **Key words: elk, temperature, behavior, thermoregulation**

118

Gese, E. M. and S. Grothe. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. American Midland Naturalist 133:36-43. Abstract: Direct observations of coyote (*Canis latrans*) predation on large wild prey are rare. We observed nine predation attempts by coyotes on deer (*Odocoileus virginianus*) and elk (*Cervus elaphus*) during winter in Yellowstone National Park, Wyoming. Coyotes were successful in five attempts. The alpha male coyote led the attack in eight of nine observations. Snow depth was significantly deeper during successful kills compared to unsuccessful attempts. Two adult coyotes could

successfully kill calf and adult elk when there was deep snowcover and the prey was in poor nutritional condition. **Key works: elk, deer, snow, predation**

119

Giacometti, M., R. Willing, and C. Defila. 2002. Ambient temperature in spring affects horn growth in male alpine ibex. Journal of Mammalogy 83(1):245-251. Abstract: Horn growth in the *Caprinae* is affected by several factors including age and nutrition, and analysis of annual horn increments can be used to interpret past events. We documented patterns of horn growth in male alpine ibexes (*Capra ibex ibex*) in central European Alps and analyzed relationships between annual horn increments, weather, and plant phenology in 2 different climatic regions during 1981-1990. Age accounted for 50% of total variance in horn growth in male alpine ibexes 1-6 years of age. Horn growth differed among climatic regions and calendar years. In years with early onset of vegetation growth, horn growth was enhanced uniformly over all age classes in both climatic regions. Horn growth was a function of ambient temperature during March-May and of plant phenology in spring, implicating onset of growth of vegetation and availability of food resources. Duration of growth of vegetation was assumed to be directly related to date of vegetation onset, but further studies are necessary to test this hypothesis. **Key words: horn, ibex, nutrition, temperature**

120

Gilbert, F. F. and M. C. Bateman. 1983. Some effects of winter shelter conditions on white-tailed deer, *Odocoileus virginianus*, fawns. Canadian Field-Naturalist 97:391-400. Abstract: The behavior of 11 white-tailed deer (*Odocoileus virginianus*) fawns was observed from December 1970 through March 1971. The animals were maintained in individual pens under cover conditions that were naturally wooded, clear-cut, or clear-cut with an artificial windbreak. Commercial feed was supplied *ad libitum* and consumption measured weekly. The responses of the animals to winter climatic conditions were monitored. The deer maintained in the clear-cut pens with an artificial windbreak lost a greater percentage of their body weight, had a lower kidney fat index, and ate less relative to body weight than the deer in the other pens. Fewer opportunities for socialization by these deer was considered partially responsible for these results. Solar radiation accounted for about 28 percent of the variation in food consumption. Food intake was maximum at a mean daily ambient temperature of -15°C, minimum at -4°C and decreased below -15°C. Greater feeding and other activity occurred when skies were overcast, when the barometer was falling and when vapor pressure humidity was increasing. The location of bed sites was affected primarily by the location of deer in adjacent pens. Sites that were potentially solar exposed were selected more often on clear than overcast days. The deer in the clear-cut pens maintained trails around the periphery of their enclosures and used those portions of the trails along fences where other deer were present more than those portions where no deer were adjacent. The animals seldom moved off their trail networks when snow thickness exceeded 30 cm. Energy costs of maintenance under these free-ranging conditions were higher than those predicted from laboratory studies by a factor of 2. **Key words: white-tailed deer, temperature, snow, clouds, barometric pressure, humidity, behavior, solar radiation**

121

Gilbert, P. F., O. C. Wallmo, and R. B. Gill. 1970. Effect of snow depth on mule deer in Middle Park, Colorado. Journal of Wildlife Management 34(1):15-23. Abstract: The distribution of mule deer (*Odocoileus hemionus*) on their winter range in Middle Park, north-central Colorado, is largely governed by snow depth. Snow over 18 inches deep essentially precludes deer use. In two of three winters of study, over 90 percent of the winter range was excluded from use because of snow. Fluctuations in winter deer counts were negatively correlated with November-February precipitation. **Key words: mule deer, precipitation, snow, habitat use**

122

Ginnett, T. F. and E. L. B. Young. 2000. Stochastic recruitment in white-tailed deer along an environmental gradient. Journal of Wildlife Management 64(3):714-720. Abstract: Texas encompasses a strong precipitation gradient from arid deserts (<370 mm) in the west to mesic pine forests (>1,300 mm) in the east. We examined the relationship between fawn recruitment in white-tailed deer (*Odocoileus virginianus*), as estimated by fall census data, and same-year precipitation along this environmental gradient. Census data for the years 1977-95 were obtained from the Texas Parks and Wildlife Department. Precipitation data covering the same period were obtained from the National Oceanographic and Atmospheric Administration for every official recording station in the state. Data were summarized by 8 precipitation zones, followed by exploratory regression analyses that revealed a changing pattern in recruitment along the precipitation gradient. The best model was a simple linear regression that incorporated the sum of March-July precipitation as the independent variable and recruitment expressed as fawns per 100 does as the dependent variable. In arid western Texas, recruitment was strongly and positively related to March-July precipitation totals. Moving eastward, regression slopes declined as precipitation totals increased. In eastern Texas, regression slopes indicated a negative relationship between recruitment and precipitation. Long-term average recruitment across precipitation zones in negatively correlated with long-term average precipitation. We suggest various causal explanations for these relationships. **Key words: white-tailed deer, precipitation, recruitment, model**

123

Goodson, N. J., D. R. Stevens, and J. A. Bailey. 1991. Effects of snow on foraging ecology and nutrition of bighorn sheep. Journal of Wildlife Management 55(2):214-222. Abstract: We studied foraging behavior, diet quality, and activity budgets of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) under different snow cover conditions on a Ponderosa pine (*Pinus ponderosa*)-shrub-bunchgrass range in the montane zone of Colorado. Snow 2-12 cm deep persisted for less than a day to several weeks and caused bighorn to nose or paw to reach forage. Biting rates were reduced during periods of snow cover as were dry matter intake rates, despite an increase in bite size. Percentage of green material in the diet declined as snow depth increased, as did percent protein and dry matter digestibility of diets. During periods of snow cover, bighorn shifted from feeding in open sites where greenup was advanced to feeding in areas of shrub cover, which enhances forage accessibility. Sheep partially compensated

for declines in nutrient intake rates by increasing foraging time during the day. We concluded that even small amounts of snow had an important negative effect on foraging efficiency and diet quality of bighorn and caused major changes in their foraging tactics. **Key words: wild sheep, snow, nutrition, diet, habitat use**

124

Grace, J. and N. Easterbee. 1979. The natural shelter for red deer (*Cervus elaphus*) in a Scottish glen. Journal of Applied Ecology 16:37-48. Summary: (1) The shelter afforded by the topography and vegetation of a Scottish glen was measured. The reduction of wind speed in the glen overall was as high as 42%. No single part was most sheltered, the ranking of sites depending on wind direction. Small-scale undulations in topography and a small area of woodland reduced wind speed by up to about 95%. The shelter value of dwarf shrub and herbaceous vegetation could be estimated from its height. (2) The influence of shelter on heat loss from deer was calculated, using established theory and published data. The extreme conditions, in the woodland and on the exposed hillside, were compared. It was estimated that nearly twice as much heat would be lost in the exposed position. Woodland reduced convective heat losses and radiative exchange with the cold sky. **Key words: red deer, wind, habitat use, thermoregulation**

125

Grignolio, S., I. Rossi, B. Bassano, F. Parrini, and M. Apollonio. 2004. Seasonal variations of spatial behaviour in female Alpine ibex (*Capra ibex ibex*) in relation to climatic conditions and age. Ethology Ecology & Evolution 16:255-264. Abstract: The spatial behaviour of female Alpine ibex *Capra ibex ibex* L. 1758, was analysed in Gran Paradiso National Park (Italy). Data collected on 14 radio-collared females from September 2000 to August 2002, using radio-tracking and direct observations. Seasonal spatial behaviour was influenced by environmental conditions, in particular climatic factors. In the presence of thick snow cover, females significantly reduced winter home range sizes. Snow cover limited ibex mobility and reduced localization altitudes. Annual home range and winter home range sizes were inversely related to age. Temperature modified the use of space by females during summer. During the hottest summer females moved over larger ranges at higher altitudes. Annual home range sizes (mean 186.2 ha ±71.7 in 2000 and 182.2 ha ± 70.0 in 2001) and seasonal home range sizes were significantly smaller than those of reintroduced populations, moreover they were smaller than those of males calculated in a close study area in Gran Paradiso National Park. **Key words: ibex, snow, temperature, behavior, movement**

126

Grinnell, J. and T. I. Storer. 1924. Animal life in the Yosemite. University of California Press, Berkeley. Regarding mule deer (*Odocoileus hemionus hemionus*) they noted “The two factors controlling the local distribution of deer in the Yosemite are the presence of the right kind of brush for food and shelter, and the absence of deep snow (p. 232)” “When these [preferred] shrubs are covered with snow, or surrounded by snow more than 18 inches deep, the animals are unable to feed. Their [seasonal]

altitudinal migrations seem to be entirely controlled by snowfall; they ordinarily remain in the high mountains in the fall until the first snow of the season sends them downhill and concentrates them. As a rule, they do not stay where the snow lies to a depth of more than 1.5 feet, but, other conditions permitting, they do remain just below this level." And again, "If the first snow is a heavy one the deer leave the altitudes with a rush" (p. 233) [a heavy one appears to be 10-12 inches or more]. The authors also show that there are migratory and non-migratory deer populations and that they winter on "sunny, snow-free, south-facing slopes" (p. 233). (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver, BC, Canada, pp. 25-26.) **Key words: mule deer, snow, movement, habitat use**

127

Grøtan, V., B-E Saether, F. Filli, and S. Engen. 2008. Effects of climate on population fluctuations of ibex. Global Change Biology 14:218-228. Abstract: Predicting the effects of the expected changes in climate on the dynamics of populations require that critical periods for climate-induced changes in population size are identified. Based on time series analyses of 26 Swiss ibex (*Capra ibex)* populations, we show that variation in winter climate affected the annual changes in population size of most of the populations after accounting for the effects of density dependence and demographic stochasticity. In addition, precipitation during early summer also influenced the population fluctuations. This suggests that the major influence of climate on ibex population dynamics operated either through loss of individuals during winter or early summer, or through an effect on fecundity. However, spatial covariation in these climate variables was not able to synchronize the population fluctuations of ibex over larger distances, probably due to large spatial heterogeneity in the effects of single climate variables on different populations. Such spatial variation in the influence of the same climate variable on the local population dynamics suggests that predictions of influences of climate change need to account for local differences in population dynamical responses to climatic conditions. **Key words: ibex, population dynamics, fecundity, mortality**

128

_____, B-E Sæther, S. Engen, E. J. Solberg, J.D.C. Linnell, R. Andersen, H. Brøseth, and E. Lund. 2005. Climate causes large-scale spatial synchrony in population fluctuations of a temperate herbivore. Ecology 86(6):1472-1482. Abstract: Theoretical analyses have shown that the spatial scaling of environmental autocorrelation, strength of density regulation, and the dispersal of individuals determine the scaling of synchrony in population fluctuations. By modeling the separate effects of density regulation, environmental stochasticity, and demographic stochasticity, we estimate the spatial scaling of the component that is due to environmental stochasticity in the population dynamics of roe deer (*Capreolus capreolus*) in Norway.

The estimated spatial scaling of the environmental noise was ~200 km. An examination of how different weather variables influenced the scaling indicated that snow depth was the major weather variable affecting the scaling of synchrony in population fluctuations, and was negatively related to population growth rates in 97.4% of the 151 populations included in the study. A large-scale climatic phenomenon, the North Atlantic Oscillation, was positively related to population growth rates in 94.7% of

the populations but did not significantly affect the pattern of synchrony among populations.

We used newly developed theoretical results of the contribution of environmental noise and dispersal to the spatial scale of synchrony to show that the spatial scaling estimated in this study could not be explained by dispersal. This suggests that common environmental noise operating mainly during the winter is able to synchronize population fluctuations of roe deer over large distances. **Key words: roe deer, snow, population dynamics, NAO, model, movement**

129

Guinness, F. E., T. H. Clutton-Brock, and S. D. Albon. 1978. Factors affecting calf mortality in red deer (*Cervus elaphus*). Journal of Animal Ecology 47:817-832.
Summary: Changes in winter (but not summer) mortality were correlated with increasing population density of hinds in the study area. **Key words: red deer, mortality, snow, nutrition, density**

130

Hagemoen, R. I. M. and E. Reimers. 2002. Reindeer summer activity pattern in relation to weather and insect harassment. Journal of Animal Ecology 71:883-892.
Summary: (1) During the brief growing season in Arctic and high mountain ecosystems, undisturbed grazing is crucial in order to maximize growth and fattening. During summer 1997 we investigated the influence of weather and insect harassment on the behaviour and group dynamics of reindeer (*Rangifer tarandus tarandus* L.). (2) Climatic data, activity of parasitic flies, and female reindeer behaviour were recorded from two wild reindeer populations in southern Norway. Temperature and solar irradiation were good predictors of oestrid fly activity. Throughout the warm summer, reindeer were exposed to vigorous oestrid fly harassment, which caused dramatic decrease in feeding and lying, and increase in walking, running and standing. This behavioural change may compromise the physical condition of individuals entering winter. (3) Mosquitoes had little influence on reindeer activity patterns. In the absence of oestrid flies, weather parameters had no influence on reindeer activity pattern. Even during the warmest days, no signs of heat stress were recorded. Accordingly, snow patches, marshes and windy mountaintops were used primarily to avoid oestrid fly harassment. Thus, most disruptions of feeding that are often reported on warm days are responses to oestrids, not thermal stress. **Key words: reindeer, insects, temperature, snow, behavior, solar radiation**

131

Hamlin, K. L. and R. J. Mackie. 1989. Mule Deer in the Missouri River Breaks, Montana: A study of population dynamics in a fluctuating environment. Final Research Project Report, Montana Department of Fish, Wildlife & Parks, Helena.
Notes: The authors noted that drought conditions resulted in low fawn survival. Survival of fawn cohorts coincided with improved forage conditions initiated by heavy rains and an autumn “green-up” of vegetation. Prior forage conditions played an important role in fawn mortality during severe winters. For example, high fawn mortality during winter 1964-65 occurred when forage conditions had been poor for 3 of the 4 prior summers

and deer were probably in relatively poor condition entering winter. Forage use during winter usually depended upon 2 major factors: snow depth and forage use during autumn. Deep snow reduces availability and use of shrubs such as rubber rabbitbrush. An autumn green-up prolonged the period of good to adequate nutrition not only through autumn, but into winter. Conversely, drought led to earlier maturation and desiccation of all herbage and in turn to heavy utilization of preferred browse, decreasing its availability during winter. During occasional winters of deep, continuous snow cover, much of the area was not inhabitable by deer, leading deer to migrate northward to areas of greater relief with steep south-facing slopes characteristically with poor forage resources. Paradoxically, effectively long winters (periods of negative energy balance), were often the result of hot dry springs, summers and autumns rather than deep snow and cold temperature during the calendar months of winter. Dry conditions during spring through autumn resulted in earlier than normal and heavy use of rubber rabbitbrush and snowberry which led to unseasonably early dependence on big sagebrush and Rocky Mountain juniper. The nutritional quality of the mule deer diet was influenced at least as much by the density-independent factor of climate as by the number of deer competing for forage. Weather certainly acted with more regularity than intraspecific competition on the nutritional quality of the deer's diet. **Key words: mule deer, diet, snow, drought, mortality, nutrition**

132

_____, S. J. Riley, D. Pyrah, A. R. Dood, and R. J. Mackie. 1984. Relationships among mule deer fawn mortality, coyotes and alternate prey species during summer. Journal of Wildlife Management 48(2):489-499. The extent, timing, and causes of summer mortality of mule deer (*Odocoileus hemionus*) fawns were studied in relation to coyote (*Canis latrans*) population level, alternate prey population levels, and coyote food habits. Additionally, fawn mortality rates were related to supplementary information on vegetation production and fawn hiding cover. A minimum of 90% of summer mortality of fawns was the result of predation by coyotes. Fawn mortality was lowest when microtine rodent populations were high. Mortality rate of fawns was not directly related to population levels of coyotes, deer mice (*Peromyscus maniculatus*), white-tailed jack rabbits (*Lepus townsendii*), or Nuttall's cottontails (*Sylvilagus nuttallii*). Vegetation production and winter snow cover may have been factors regulating microtine populations and thereby fawn mortality rates. Coyote predation can reduce fawn survival in nutritionally healthy deer populations, but alternate prey population levels and cycle phase should be determined by managers prior to decisions about predator control to increase deer populations. **Key words: mule deer, snow, mortality**

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Harestad, A. S. and F. L. Bunnell. 1979. Snow and its relationship to deer and elk in coastal forests. Report to B. C. Council of Forest Industries. A synthesis paper assessing effects of snow on energy expenditure and acquisition and the effects of forestry practices on snowpack characteristics and winter habitat of deer and elk. Energy expenditure for movement through a range of depths was determined from a linear regression equation. Sinking depth was calculated as a function of snow density and morphological characteristics. Three-dimensional plots are presented of energy expenditure vs snow density vs snow depth. Effect of snow on availability of forage is

discussed. The major effects of snow on forage availability are a) to exceed vegetation height, b) displace the vegetation down into the snowpack, and c) to allow animals to stand higher above ground level and hence reach previously unavailable browse. The vertical distribution of browse differs between old-growth timber and clearcuts. In dense forest, 50-110 cm of snow is required to cover 75% of the forage whereas only 20-50 cm is sufficient on cutover areas. Litterfall is an important source of food and is enhanced by snow breakage of branches.

Using published data, a regression line is developed relating snow water equivalent in the open to the slope of the snow depth/canopy cover regression. Smaller percentages of snowfall were captured by the canopy in areas of heavier snowfall.

Snow density is an important characteristic as it affects sinking depth. Density of new snow located under tree crowns may be 42% greater than new snow in openings. This may be due to compaction of snow falling from trees. The effect applies only to new snow and snowpack density is relatively unaffected by forest cover.

The dilemma for integrated forestry-wildlife management is that increasing crown closure, while reducing snow depth and energy expenditure for movement, will also reduce understory vegetation. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver, BC, Canada, pp. 27-28.) **Key words: black-tailed deer, elk, snow, nutrition, habitat use**

134

Harper, J. A., J. H. Harn, W. W. Bentley, and C. F. Yocom. 1967. The status and ecology of Roosevelt Elk in California. Wildlife Monograph No. 16. The Wildlife Society. The authors note the influence of weather on movements and activities of elk. Bugling and rutting battles took place largely during the cold evenings. In some cases strong winds excluded elk from wooded areas because of branches and foliage falling from the trees. Cold rains during the calf drops of 1957 and 1960 may have been a factor in the calf survival rate. Feeding was also affected by weather. On calm days with little wind, relative humidity in the 60s and 70s and warm air temperature, elk would feed steadily, moving only to locate plants. On rainy days or days of falling barometric pressure elk would feed sporadically, moving rapidly from plant to plant. Linear distance covered on these days was often 3 to 4 times greater than that covered on calm days. **Key words: elk, wind, temperature, precipitation, barometric pressure, behavior**

135

Hart, J. S., O. Heroux, W. H. Cottle, and C. A. Mills. 1961. The influence of climate on metabolic and thermal responses of infant caribou. Canadian Journal of Zoology 39(6):845-856. Abstract: Metabolic and thermal responses of infant caribou to climate were measured during the June calving period on the barrens in the area of Mosquito Lake and Beverly Lake, N.W.T. It was found that temperature regulation was well established at birth and that the calves were very sensitive metabolically to cold, wind, and precipitation. The metabolic rate was doubled by a lowering of temperature to about 0°C, but cold combined with wind and precipitation elevated the metabolic rate to over five times the resting value. Calves which were exposed without protection to such conditions eventually became hypothermic and died. Weather conditions during storms on the barrens are sufficiently severe to produce some mortality in animals exposed without protection. The possibilities for prediction of mortality from wind chill values and

estimated fur heat loss are discussed. **Key words: temperature, caribou, wind, mortality, thermoregulation**

136

Hass, C. C. 1997. Seasonality of births in bighorn sheep. Journal of Mammalogy 78(4):1251-1260. Abstract: Two populations of bighorn sheep (*Ovis canadensis*) in contrasting habitats at the same latitude were studied for 3 years to examine effects of climate and nutrition on seasonality of births. The number of births peaked during February and March in the Mojave Desert and during mid-June in the Rocky Mountains. Yearly differences in seasons of birth were apparent in the Mojave Desert, but not in the Rocky Mountains. Comparisons with captive and transplanted populations revealed that desert subspecies of bighorn sheep gave birth earlier in the year and had longer seasons of birth than northern subspecies. Bighorn sheep appear to give birth when temperature and nutrition are most conducive to survival of offspring. **Key words: wild sheep, temperature, parturition, nutrition**

137

Hebblewhite, M. 2005. Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. Journal of Animal Ecology 74:226-233. Summary: 1. Recent research reveals the widespread influence of the North Atlantic Oscillation (NAO), a large-scale climatic variation, on northern ungulate populations. Little is known, however, about the influence of the North Pacific Oscillation (NPO), a similar climatic index, on ungulates. 2. The influence of the NPO on elk population dynamics in Banff National Park (BNP) was examined using a 15-year time-series of three elk subpopulations exposed to different levels of predation by wolves. NPO was strongly related to local climate data including snow depth (r=+0·61) and winter temperatures (r=-0·51). 3. Higher NPO values reflected increasing winter severity, reducing elk population growth rate irrespective of wolf-predation pressure. Elk population growth rate, however, declined more strongly in areas with wolf predation through the interaction with winter severity, indexed by NPO. Effects of NPO were weaker in the absence of wolf predation. 4. Differences between the effects of snow and NPO were revealed that depended on wolf predation pressure. Without wolf predation, NPO reduced elk population growth rate, suggesting overall climate was important. With wolf predation, snow depth was more important than NPO, suggesting a mechanism of increased wolf predation rates in deeper snow. 5. This study is the first to demonstrate the influential role of Pacific climate on western North American ungulate population dynamics and provides further evidence of the role of large-scale climatic variation in terrestrial ecosystem dynamics. **Key words: elk, NPO, population dynamics, predation, snow**

138

Heimer, W. E., F. J. Mauer, and S. W. Keller. 1994. The effects of physical geography on Dall sheep habitat quality and home range size. Proceedings of the Biennial Symposium, Northern Wild Sheep and Goat Council 9:144-148. Abstract: Physical geography and prevailing macro-climatic factors determine habitat suitability for Dall sheep (*Ovis dalli*). Dall sheep habitats, which support high densities of sheep, are

found on the lee (or snow-shadowed) sides of linearly arrayed mountain ranges which lie across the routes of prevailing bulk air flow. The higher density sheep habitats within these mountains are characterized by long, straight drainages paralleling bulk air flow. These drainages channel cold, heavy dry air masses downhill after the air masses have cooled and lost the ability to carry water while being forced up and over the mountains. Wind speed increases as gravity accelerates the dense air masses downhill, producing catabatic winds in the absence of (or within) barometric pressure cells. These predictable winds prevent snow accumulation on ridges between tributaries that flow into larger drainages and produce stable wintering habitats for Dall sheep. Habitable but suboptimal ranges are found where one or more of these ideal physiographic conditions is absent and average winter snow accumulation is less than 175 cm (70 in.). Winter ranges are less stable in the suboptimal habitats. Preliminary analysis of existing data on Dall sheep movements and home range sizes suggests an inverse relationship between habitat climatic stability and winter home range size. Less stable winter habitats demand greater flexibility in use of available microhabitats by the sheep which occupy these ranges. This demand results in larger home ranges with generally less stable populations of sheep than higher quality (more climatically stable) habitats. **Key words: wild sheep, wind, temperature, habitat use, movement**

139

Helle, T. and I. Kojola. 2008. Demographics in an alpine reindeer herd: effects of density and winter weather. Ecogaphy 31:221-230. Abstract: We examined how population density, winter weather, snow conditions, and 2 large-scale climatic indices (North Atlantic Oscillation, NAO, and Arctic Oscillation, AO) influenced demography (reproduction and mortality) in an alpine herd of semi-domesticated reindeer *Rangifer tarandus* between 1959 and 2000 in Finnish Lapland. The herd lived on heavily grazed lichen pastures, with winter densities between 0.8 and 3.9 individuals km^{-2}. Icing conditions occurred every 7^{th} year, on an average, and decreased reproductive rate (calves/females) by 49%. In general linear models icing remarkably increased the fit of snow models to reproductive rate. Incorporation of an interaction term between icing and the snow depth index provided better fit than a model without interaction. Delayed snowmelt decreased reproductive rate. For the day of snowmelt, however, the model without interaction was better than the interaction model. These 3 models provided the best fit to the data and accounted for 51-54% of the variation in reproductive rate. Winter mortality was related to density and large-scale climatic indices, but not to local winter weather except a slight increase in mortality during an icing winter. The best model for winter mortality, including reindeer density and NAO, accounted for 26% of variation in mortality. Three factors may be involved explaining weak density dependence or the lack of such dependence; climate change scenarios that predict higher winter temperature, more frequent thawing-freezing periods, and deeper snow would be expected to decrease reproductive rate and increase winter mortality of reindeer and thus to reduce profitability of reindeer husbandry. In contrast, early springs would be advantageous for reindeer in the short term. **Key words: caribou, snow, ice, temperature, NAO, AO, mortality, model**

140

Henshaw, J. 1968. The activities of the wintering caribou in northwestern Alaska in relation to weather and snow conditions. International Journal of Biometeorology 12(1):21-27. When snow depths reach 25 cm, feeding ceased to be a traveling activity and became basically sedentary. Evidence is given for strong selection of local areas with shallow snow depth. In one winter, caribou rarely dug through snow harder than 65 g cm^{-2}. Caribou did not crater through snow deeper than 70 cm and rarely in snow deeper than 50 cm. Potential population numbers are limited more by snow distribution than by food quantity. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography,* University of BC, Vancouver, BC, Canada, p. 28.) **Key words: caribou, snow, distribution**

141

Hepburn, R. L. 1978. A snow penetration guage for studies of white-tailed deer and other northern mammals. Journal of Wildlife Management 42(3):663-667. The author describes the design and field testing of an instrument to measure sinking depth of snow traversed by cervids. **Key words: white-tailed deer, snow, technique**

142

Herfindal, I., B-E Saether, E. J. Solberg, R. Andersen, and K. A. Høgda. 2006. Population characteristics predict responses in moose body mass to temporal variation in the environment. Journal of Animal Ecology 75:1110-1118. Summary: 1. A general problem in population ecology is to predict under which conditions stochastic variation in the environment has the stronger effect on ecological processes. By analyzing temporal variation in a fitness-related trait, body mass, in 21 Norwegian moose *Alces alces* (*L*.) populations, we examined whether the influence of temporal variation in different environmental variables were related to different parameters that were assumed to reflect important characteristics of the fundamental niche space of the moose. 2. Body mass during autumn was positively related to early access to fresh vegetation in spring, and to variables reflecting slow phenological development (low June temperature, a long spring with a slow plant progression during spring). In contrast, variables related to food quantity and winter conditions had only a minor influence on temporal variation in body mass. 3. The magnitude of the effects of environmental variation on body mass was larger in populations with small mean body mass or living at higher densities than in populations with large-sized individuals or living at lower densities. 4. These results indicate that the strongest influence of environmental stochasticity on moose body mass occurs towards the borders of the fundamental niche space, and suggests that populations living under good environmental conditions are partly buffered against fluctuations in environmental conditions.**Key words: moose, index, nutrition**

143

Hetem, R. S., S. K. Maloney, A. Fuller, L. C. R. Meyer, and D. Mitchell. 2007. Validation of a biotelemetric technique, using ambulatory miniature black globe thermometers, to quantify thermoregulatory behavior in ungulates. Journal of Experimental Zoology Part 307(6):342-356. Abstract: Behavioral thermoregulation is

an animal's primary defense against changes in the thermal environment. We aimed to validate a remote technique to quantify the thermal environment behaviorally selected by free-ranging ungulates. First, we demonstrated that the temperature of miniature, 30 mm diameter black globes (miniglobes) could be converted to standard 150 mm diameter black globe temperatures. Miniglobe temperature sensors subsequently were fitted to collars on three free-ranging ungulates, namely blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*) and horse (*Equus caballus*). Behavioral observations were reflected in animal miniglobe temperatures which differed from those recorded by an identical miniglobe on a nearby exposed weather station. The wildebeest often selected sites protected from the wind, whereas the impala and the horse sheltered from the sun. Nested analysis of variances revealed that the impala and horse selected significantly less variable environments than those recorded at the weather station ($P<0.001$) over a 20-min time interval, whereas, the microclimates selected by wildebeest tended to be more variable ($P=0.08$). Correlation of animal miniglobe against weather station miniglobe temperature resulted in regression slopes significantly less than one ($P<0.001$) for all species studied, implying that, overall, the animals selected cooler microclimates at high environmental heat loads and/or warmer microclimates at low environmental heat loads. We therefore have developed an ambulatory device which can be attached to free-ranging animals to remotely quantify thermoregulatory behavior and selected microclimates. **Key words: index, temperature, behavior, thermoregulation**

144

Hik, D. S. and J. Carey. 2002. Spatial and temporal synchrony in horn growth of Dall sheep rams in the Yukon. Proceedings Northern Wild Sheep and Goat Council 13:189. Abstract (Only): Horn growth of Dall sheep (*Ovis dalli*) rams was estimated as the volume of annual increments for 8491 individuals harvested throughout the Yukon between 1974 and 2001. We observed broad synchronization, with an approximate 10-year periodicity, in patterns of horn growth throughout the Yukon. The greatest variability and coherence in horn growth among different cohorts was observed in the southwest Yukon. In the northern Yukon, less interannual variability was observed. The largest horns were from the central Yukon. These patterns of variability between different ecological and climatic regions of the Yukon are consistent with our earlier hypothesis that horn growth of Dall sheep rams is a sensitive index of climatic variability. Periodic variation in climate, which influences availability of forage productivity in alpine environments, provides a means of predicting patterns of horn growth and has implications for management of these populations. **Key words: wild sheep, horn, index, nutrition**

145

Hoefs, M. and U. Nowlan. 1994. Distorted sex ratios in young ungulates: the role of nutrition. Journal of Mammalogy 75(3):631-636. Abstract: The long-held view that sex ratios of ungulates at birth are at or near parity has been the subject of considerable debate. Numerous examples of distorted sex ratios at birth have been reported, but the observations and their interpretation have not been consistent. Study of captive ungulates can provide valuable information on this contentious subject because relevant data are easy to obtain and are reliable. We assessed sex ratios of offspring from

ungulates held in game farms in the Yukon Territory, Canada. Elk (*Cervus elaphus nelsoni*), reindeer (*Rangifer tarandus tarandus*), mountain goats (*Oreamnus americanus*), Dall's sheep (*Ovis dalli dall*i), Stone's sheep (*Ovis dalli stonei*), and caribou (*Rangifer tarandus caribou*) were studied. Sample sizes among these species varied from 11 to 320 young, and observation periods varied between 2 and 23 years. All six ungulates showed a distorted sex ratio of neonates favoring females, which we attribute to the high-quality supplementary feed provided to these animals. **Key words: elk, caribou, mountain goat, wild sheep, sex ratio, nutrition**

146

Holter, J. B., W. E. Urban, Jr., H. H. Hayes, H. Silver, and H. R. Skutt. 1975. Ambient temperature effects on physiological traits of white-tailed deer. Canadian Journal of Zoology 53(6):679-685. Abstract: Six adult white-tailed deer (*Odocoileus virginianus borealis*) were exposed to 165 periods of 12 consecutive hours of controlled constant ambient temperature in an indirect respiration, calorimeter. Temperatures among periods varied from 38 to 0 (summer) or to -20C (fall, winter, spring). Traits measured were energy expenditure (metabolic rate), proportion of time spent standing, heart rate, and body temperature, the latter two using telemetry. The deer used body posture extensively as a means of maintaining body energy equilibrium. Energy expenditure was increased at low ambient temperature to combat cold and to maintain relatively constant body temperature. Changes in heart rate paralleled changes in energy expenditure. In a limited number of comparisons, slight windchill was combated through behavioral means with no effect on energy expenditure. The reaction of deer to varying ambient temperatures was not the same in all seasons of the year. It is apparent from this study that the white-tailed deer uses a number of physiological and behavioral responses, depending on season and the status of its hair coat at the time, to compensate for adverse conditions of ambient temperature and mild wind chill. The evidence suggests that this species is remarkably adaptable to rather rapid changes in ambient temperature which lead to unfavorable conditions in its environment, and may not necessarily respond to these conditions in the same manner as other ruminant species or in a similar way during all seasons of the year. **Key words: white-tailed deer, temperature, wind, behavior**

147

Hone, J. and T. H. Clutton-Brock. 2007. Climate, food, density, and wildlife population growth rate. Journal of Animal Ecology 76:361-367. Summary: 1. The aim of this study was to derive and evaluate *a priori* models of the relationship between annual instantaneous population growth rate (*r*) and climate. These were derived from the numerical response of annual *r* and food, and the effect of climate on a parameter in the numerical response. The goodness of fit of a range of such deductive models to data on annual *r* of Soay sheep and red deer were evaluated using information-theoretic (AICc-based) analyses. 2. The analysis for sheep annual *r* showed negative effects of abundance and negative effects of the interaction of abundance an climate, measured as March rainfall (and winter NAO) in the best fitting models. The analysis for deer annual *r* showed a negative effect of deer abundance and a positive effect of climate measured as March rainfall (but a negative effect of winter NAO), but no interaction of abundance and climate in the best fitting models. 3. There was most support in the

analysis of sheep dynamics for the ratio numerical response and the assumption that parameter *J* (equilibrium food per animal) was influenced by climate. In the analysis of deer dynamics there was most support for the numerical responses assuming effects of food and density (Ivlev and density, food and density, and additive responses) and slightly less support for the ratio numerical response. The evaluation of such models would be aided by the collection of and incorporation of food data into the analyses. **Key words: red deer, Soay sheep, population dynamics, snow, precipitation, NAO, model, nutrition**

148

Hosley, N. W. 1956. Management of white-tailed deer in its environment. Pp. 187-259 in W. P. Taylor, ed. The deer of North America. The Stackpole Company, Harrisburg, PA. Snow depths greater than about 20 inches make white-tailed deer travel by jumps. Height of a fawn's breast is 18-19 inches vs 20-22 for an adult. **Key words: white-tailed deer, snow, movement**

149

Hovey, F. W. and A. S. Harestad. 1992. Estimating effects of snow on shrub availability for black-tailed deer in southwestern British Columbia. Wildlife Society Bulletin 20(3):308-313. Abstract: Snow can restrict use of winter habitat by Columbian black-tailed deer (*Odocoileus hemionus columbianus*) by reducing availability of forage. Effects of snow on forage availability has received little attention. Forage availability during winter has been estimated by functions that use differences between total snow depth or mean snow depth and prewinter plant height distribution. The important assumption of this method is that snow deposition does not affect plant height. This assumption may not be correct. Because most forage plants are usually flexible, they are often displaced downwards by snow and by changes in depth and composition of the snowpack. Important black-tailed deer forage species such as salal (*Gaultheria shallon*) and huckleberries (*Vaccinium parvifolium* and *V. ovalifolium*) can intercept snow and are vulnerable to height displacement and burial. We estimated these effects for both huckleberries and salal, measured displacement and burial, and developed regression equations predicting available height from measures of snow depth and prewinter plant height. **Key words: black-tailed deer, snow, nutrition**

150

Høye, T. T. and M. C. Forchhammer. 2006. Early developed section of the jaw as an index of prenatal growth conditions in adult roe deer *Capreolus capreolus*. Wildlife Biology 12(1):71-76. Abstract: Increasing evidence suggests that conditions in early life have important consequences for ultimate body size and fitness. Skeletal parts are often used as retrospective indices of body size and growth constraints because of their resistance to seasonal variation in resource availability. Yet, slow-maturing bones are poor predictors of resource limitations during early development, as later benign conditions may lead to compensatory growth. We analyzed the temporal growth dynamics of different sections of the lower jaw of roe deer *Capreolus capreolus* and found that the medioanterior section of the lower jaw reaches 95% of asymptotic size already at 2-4 months post partum, whereas the posterior section reaches 95% of

asymptotic size at 14-16 months post partum. Hence, the size of the medioanterior section of the lower jaw is only dependent on resource availability *in utero* and the first few months *post partum* and, as such, potentially leaves a fingerprint of prenatal growth conditions that is evident even in adult individuals. This supports earlier findings in ungulates of a shift in skeletal growth spurts after weaning, and suggests that the choice of skeletal index for population and cohort studies is not trivial. **Key words: index, roe deer**

151

Huggard, D. J. 1993. Effect of snow depth on predation and scavenging by gray wolves. Journal of Wildlife Management 57(2):382-388. Abstract: Snow can affect wolf predation rates, diet composition, and scavenging, which are important components in understanding and managing wolf-prey systems. Thus, I located elk (*Cervus elaphus*) killed by gray wolves (*Canis lupus*, hereafter referred to as wolves) in Banff National Park, Alberta for 5 winters, and I followed one pack of wolves intensively throughout 1 winter to determine the effects of snow depth on wolf predation. Kill rate increased (P <0.001) from 1 ungulate/5.4 days with no snow to 1 ungulate/1.1 days in snow 60 cm deep. Similar (P >0.5) numbers of calves (n = 24) and adults (n = 28) were killed in shallow snow; predominantly calves (9 of 11) were killed at intermediate snow depths that hindered calves but not adults; and only adults (n = 9) were killed in deep snow that hindered both age classes of elk. Scavenging of ungulate carcasses occurred at shallower (P < 0.01) snow depths than did kills. At shallow snow depths, wolves likely encountered carcasses more frequently because they had a lower kill rate and moved farther between kills. My data indicate snow depth could add substantial, density-independent variation to wolf-prey interactions and affect which classes of prey are killed. **Key words: elk, snow, predation**

152

Hutchinson, C. F., S. E. Marsh, B. Orr, P. Krausman, R. M. Enns, L. Howery, E. Pfirman, C. Wallace, J. Walker, K. Mauz, H. Boyd, and H. Salazar. 2001. Informing the elk debate: applying NASA Earth Observing System (EOS) Data to natural resource management conflicts in the western states *in* Geoscience and Remote Sensing Symposium, IGARSS'01 IEEE International 2:834-836. Abstract: This study was designed to provide information that might help resource managers understand the distribution of elk in Arizona as a consequence of seasonal variation and in response to extreme climatic events (i.e. El Niño and La Niña). The first task involved modeling elk populations over time. A technique for modeling elk population has been developed that is based on harvest data, estimates of elk populations for individual game management units (areas for which harvest is reported and within which elk are managed by the Arizona Game and Fish Department). The second task involved the use of satellite data to characterize vegetation responses to seasonal and interannual climate variation among vegetation associations within game management units. This involved the use of NOAA-AVHRR time series data to describe temporal vegetation behavior, Landsat data to describe spatial vegetation distribution in conjunction with U.S. Forest Service vegetation maps. Elk population estimates were correlated with satellite-derived vegetation measures by vegetation association through time. The patterns of elk distribution that this revealed were complex. Not surprisingly, animals appear to respond

to differences in vegetation availability—both seasonally and interannually—as portrayed by satellite data. **Key words: elk, EOS, Landsat, distribution, El Niño, La Niña, distribution, nutrition, model**

153

Jacobson, A. R., A. Provenzale, A. Von Hardenberg, B. Bassano, and M. Festa-Bianchet. 2004. Climate forcing and density dependence in a mountain ungulate population. Ecology 85(6):1598-1610. Abstract: Population models in ecology are rarely validated by comparing their predictions to long-term observations of changes in population size. We have used a variety of analytical tools to examine a 45-year time series of annual censuses of Alpine ibex (*Capra ibex*) on the Gran Paradiso National Park in northwestern Italy. This ibex population grew from about 3300 to almost 5000 individuals in the 1980s during a decade of anomalously mild winters, and then began to decline in the 1990s. By 1997, the population size had returned to previous levels. Adult survival apparently increased and adult sex ratio may have changed to slightly favor males during the increase in population density. Yearly changes in total population were correlated with seasonal average snow depth and population density over the 39 years for which climate data were available. Our results show that the ibex population size was limited by both density dependence and deep snow. A model based on these factors fit to the first 19 years of data was used to forecast subsequent changes in total population based on initial population size and yearly snow depth. The model was able to predict the increase and subsequent decline in total population size over the final 20 years of the study but failed to reproduce population levels after the eruption. Our results suggest that the 1980s episode of population growth was primarily driven by increased adult survival, rather than increased recruitment. **Key words: ibex, snow, population dynamics**

154

Jedrzejewk, W., B. Jedrzejewka, H. Okarma, and A. L. Ruprecht. 1992. Wolf predation and snow cover as mortality factors in the ungulate community of the Bialowieza National Park, Poland. Oecologia 90(1):1432-1939. Abstract: Wolf-ungulate interactions were studied in the pristine deciduous and mixed forests of the Bialowie, a national park, in 1985-1989. The study period included two severe and two mild winters. The community of ungulates inhabiting Bialowie, a national park, consisted of red deer *Cervus elaphus*, 55% of all ungulates; wild boar *Sus scrofa*, 42%; and roe deer *Capreolus capreolus*, moose *Alces alces*, and European bison *Bison bonasus*, about 1% each. The average size of red deer groups increased from 2.7 (SD 2.35) in spring and summer to 6.9 (SD 6.84) in autumn and winter. In winter the group size of red deer was positively correlated with the depth of snow cover and negatively correlated with the mean daily temperature. Average group size of wild boar did not change significantly between seasons; it was 6.8 (SD 5.16) in spring and summer and 5.7 (SD 4.67) in autumn and winter. Analysis of 144 wolf scats showed that wolves preyed selectively on red deer. In October-April, *Cervidae* (mostly red deer) constituted 91% of biomass consumed by wolves, while wild boar made up only 8%. In May-September deer formed 77% of prey biomass, and the share of wild boar increased to 22%. In all seasons of the year wolves selected juveniles from deer and boar populations; 61% of red deer and 94% of wild boar of determined age recovered from wolves' scats were

young <1 year old. Analysis of 117 carcasses of ungulates found in Bialowie, a national park, showed that predation was the predominant mortality factor for red deer (40 killed, 10 dead from causes other than predation) and roe deer (4 killed, none dead). Wild boar suffered most from severe winter conditions (8 killed, 56 dead). The percentage of ungulates that had died from under nutrition and starvation in the total mortality was proportional to the severity of winter. **Key words: red deer, roe deer, snow, mortality**

155

Jenkins, E. J. 2005. Ecological investigation of a new host-parasite relationship: *Parelaphostrongylus odocoilei* in thinhorn sheep (*Ovis dalli*). Thesis, University of Saskatchewan, Saskatoon, Saskatchewan, Canada. Abstract: Discovery of a new host-parasite relationship, *Parelaphostrongylus odocoilei* in Dall's sheep (*Ovis dalli dalli*) in the Canadian North, prompted the first investigation of the geographic distribution, pathogenesis, ecology and epidemiology of this parasite, as well as the related protostrongylid *Protostrongyus stilesi*, at Subarctic latitudes (60-65°N). All protostrongylid parasites have an indirect life-cycle, where first-stage larvae are shed in the feces of a mammalian definitive host, penetrate the foot of a gastropod intermediate host, and develop to infective third-stage larvae.

Protostrongylid larvae were recovered from over 2000 fecal samples form thinhorn sheep (*Ovis dalli*) and other hosts for *P. odocoilei* and *P. stilesi* across northwestern North America (38-69°N). Through novel application of molecular techniques to identify morphologically indistinguishable first-stage larvae, new records for *P. odocoilei* were established at 20 loctaions. This provided insight into the historical origins and biogeography of this new host-parasite relationship, and greatly expanded the known geographic range of both protostrongylids.

Clinical effects, including a neurological syndrome, were described in five thinhorn sheep experimentally infected with *P. odocoilei*. Neural and respiratory pathology in these five sheep were compared with over 50 wild Dall's sheep from a population naturally infected with *P. odocoilei* and *P. stilesi*. In the end stages, diffuse verminous interstitial pneumonia associated with *P. odocoilei* led to respiratory failure, and may have acted as a predisposing factor for bacterial pneumonia, which caused sporadic mortalities in this wild population.

At Subarctic latitudes, seasonal patterns in host and parasite availability, including larval shedding by Dall's sheep and larval development in experimentally infected gastropods, suggested that lambs become infected with *P. odocoilei* in a narrow seasonal window in their first fall on winter range. In combination with laboratory experiments, a degree day model for temperature-dependent larval development was developed, validated, and applied to describe and predict the effects of climate warming on protostrongylid parasites of thinhorn sheep in northern North America. In a future of climate warming, the narrow seasonal window for parasite development and transmission would be significantly extended, leading to amplification of populations of *P. odocoilei* and *P. stilesi* in endemic regions, and possibly range expansion of *P. odocoilei.* This may have consequences for the health of thinhorn sheep, as well as other wildlife that are important resources in the Canadian North. **Key words: wild sheep, disease, temperature**

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_____, A. M. Veitch, S. J. Kutz, E. P. Hoberg, and L. Polley. 2006. Climate change and the epidemiology of protostrongylid nematodes in northern ecosystems: *Parelaphostrongylus odocoilei* and *Protostrongylus stilesi* in Dall's sheep (*Ovis d. dalli*). Parasitology 132:387-401. Summary: We describe the epidemiology of the protostrongylid parasites *Parelaphostrongyls odocoilei* and *Protostrongylus stilesi* in Dall's sheep (*Ovis dalli dalli*) from the Mackenzie Mountains, Northwest Territories, Canada (65°N; 128°W). Peak numbers of 1st-stage larvae of both parasites were shed by Dall's sheep on their winter range from March until May. In larval development experiments in the Mackenzie Mountains, peak numbers of infective 3rd-stage larvae of *P. Odocoilei* were available in gastropod intermediate hosts in August-September. For both protostrongylids, the majority of transmission likely occurs on the winter range, with infection of gastropods when they emerge from hibernation in spring, and infection of Dall's sheep upon their return in fall. We validated a degree-day model for temperature-dependent development of larval *P. odocolei* in gastropods, and applied degree day models to describe and predict spatial and temporal patterns in development of *P. odocoilei* and *P. stilesi* in northern North America. Temperature-dependent larval development may currently limit northward range expansion of *P. odocoilei* into naïve populations of Dall's sheep in the Arctic, but climate warming may soon eliminate such constraints. In Subarctic regions where both *P. odocoilei* and *P. stilesi* are endemic, the length of the parasite 'growing season' (when temperatures were above the threshold for larval development) and amount of warming available for parasite development has increased over the last 50 years. Further climate warming and extension of the seasonal window for transmission may lead to amplification of parasite populations and disease outbeaks in host populations. **Key words: wild sheep, disease, temperature**

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Jenkins, K. J. and N. L. Barten. 2005. Demography and decline of the Mentasta caribou herd in Alaska. Canadian Journal of Zoology 83: 1174-1188. Abstract: We evaluated population trends in the Mentasta caribou (*Rangifer tarandus* (L., 1758)) herd in Wrangell St. Elias National Park and Preserve, Alaska, from 1990 to 1997 and determined factors contributing to its decline. We postulated that predation-related mortality of adult females and juveniles was the proximate cause of the decline, and that survival of juvenile caribou reflected interactions with winter severity, calving distribution, timing of births, density of caribou, and physical condition of neonates at birth. The population declined at its greatest rate from 1990 to 1993 (r = -0.32) and at a lower rate from 1994 to 1997 (r = -0.09). Recruitment (number of calves/100 females during September) averaged 4/100 during the rapid population decline from 1990 to 1993 and 13/100 from 1994 to 1997. Parturition rate of adult females ranged from 65% to 97%. Survival of adult females and juveniles ranged from 0.77 to 0.86 and from 0.00 to 0.22, respectively. Approximately 43%, 59%, and 79% of all juvenile mortality occurred by 1, 2, and 4 weeks of age, respectively. We confirmed predation-related mortality as the primary proximate cause of population decline, with gray wolves (*Canis lupus* L., 1758), bears (species of the genus *Ursus* L., 1758), and other predators accounting for 57%, 38%, and 5%, respectively, of all juvenile mortality, and bears causing disproportionate mortality among 0- to 1-week-old neonates. We supported the hypotheses that timing of birth and habitat conditions at the birth site, particularly mottled snow patterns, affected

vulnerability and survival of neonates, and birth mass affected survival of juveniles through summer. We speculate that the population will continue to decline before reaching a low-density equilibrium that is sustained by density-dependent changes in the functional responses of predators. **Key words: caribou, mortality, snow, predation**

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_____ **and G. Wright. 1987. Dietary niche relationships among cervids relative to winter snowpack in northwestern Montana. Canadian Journal of Zoology 65:1397-1401.** Abstract: We compared diets of white-tailed deer (*Odocoileus virginianus ochrourus*), Rocky Mountain elk (*Cervus elaphus nelsoni*), and Shiras moose (*Alces alces shirasi*) during two winters in the North Fork of the Flathead Valley, Montana. Diets of white-tailed deer contained the greatest proportions of low-lying evergreen shrubs, as well as high proportions of coniferous browse. Elk selected greater proportions of grasses than did white-tailed deer or moose, whereas moose consumed the greatest proportion of deciduous shrubs. Deep snow in 1982 increased the similarity of diets chosen by white-tailed deer, elk, and moose. In 1982, white-tailed deer and elk consumed more total browse, and moose more coniferous browse, as deep snow covered the preferred forages. Increased dietary overlap and energy limitations suggested a potential for interspecific competition during harsh winters. **Key words: white-tailed deer, elk, moose, snow, nutrition**

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Jones, G. W. 1975. Aspects of the winter ecology of blacktailed deer (*Odocoileus hemionus columbianus* Richardson) on northern Vancouver Island. M.Sc. thesis, University of B.C., Vancouver, Canada. A study of winter ecology of black-tailed deer in the Nimpkish Valley of northern Vancouver Island designed to determine the effects of clearcut logging on deer winter range.

Snow depths increased with increasing elevation in both logged and unlogged areas. Snow depths in the forest were about half as great as in clearcuts. Snow depth in feet (y) was related to crown closure in % (x) by the expression y=5.69-0.07x. Crown closure decreased with increasing elevation whereas *Vaccinium* and cedar decreased in abundance with increasing canopy cover. Vegetative cover cannot be predicted from seral type, elevation, aspect or crown closure.

In severe winters, diets were composed primarily of conifers and shrubs and are less diverse than in mild winters. Deer use of logged habitat was low when the snow was deep and soft and increased when the snow became crusted. This increase was most noticeable in second growth slash where browse was available. Track counts were not statistically well correlated with track depth or snow depth which contradicted subjective conclusions. Only timber habitats having crown closures of ≥ 65% were heavily used. Deer use was greater in timbered habitat having a shrub understory than in habitats having a conifer understory.

Chest heights, total foot areas, and foot loadings are presented. It is recommended that heavily-used winter ranges be excluded from logging plans. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver, BC, Canada, p-. 21-32.) **Key words: black-tailed deer, snow, distribution, diet**

160

Kaji, K., H. Okada, M. Yamanaka, H. Matsuda, and T. Yabe. 2004. Irruption of a colonizing Sika deer population. Journal of Wildlife Management 68(4):889-899.
Abstract: Irruptions of ungulate populations have been observed, but little is known of their cause of initiation and termination. We documented an irruption of a naturally colonizing sika deer (*Cervus nippon*) population on Cape Shiretoko, Shiretoko Peninsula, northeastern Hokkaido, Japan, and we examined limiting factors on population growth. The population increased from 54 deer in 1986 to 592 deer in 1998 (11 to 118 deer/km^2, respectively) and declined to 177 (35 deer/km^2) the following winter of 1999. The intrinsic rate of increase from 1986 to 1998 was 0.19 (95% CI: 0.16 to 0.22). We estimated an annual survival for adult females of 0.92. The ratio of calves to adult females was 76%. We observed a density-correlated reduction in winter food resources. Density-dependent food resources and their interaction with climatic factors were the most important limiting factors for sika deer. The population recovered rapidly following the population crash in 1999 and increased to 512 deer (102 deer/km^2) in 2002. We anticipate further increase and a second crash. To confirm whether the population will be regulated naturally and to establish sika deer management policy in Shiretoko National Park, long-term monitoring of the relationship between sika deer and their habitat must be implemented. **Key words: sika deer, diet**

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Keating, K. A. 1985. The effects of temperature on bighorn population estimates in Yellowstone National Park. International Journal of Biometeorology 29(1):47-55.
Abstract: The effects of temperature on bighorn population estimates for Yellowstone National Park's Mt. Evert's winter range were examined. Based on work by Houston (1982), a bipartite relationship was hypothesized, whereby the effects of temperature upon the observability of sheep was predicted to be significantly different in those portions of the temperature spectrum where snowmelt occurs. Analyses of the regressions of bighorn numbers observed on mean daily ground temperature supported this hypothesis. At temperatures less than 0°C, counts increased significantly with temperatures at a rate of 3.15:1, but were found to underestimate bighorn numbers and be unreliable as estimators of population trend. Counts conducted at 0° to 7°C increased with temperature at a significantly greater rate of 18.53:1. However, correction for population increases suggested this relationship reflected the intercorrelation of temperature and year; a result of selecting increasingly better census conditions over time. It was concluded that no additional benefit accrued from further increases in temperature once snowmelt occurred and that counts conducted at 0° to 7°C (the period between snowmelt and spring migration) were equally reliable. The importance of regarding snowmelt as a threshold value was underscored by the vastly different conclusions regarding bighorn population trends which have been drawn by different researchers from very nearly the same data. While previous research concluded that apparent population increases were the result of temperature-biased data, this study concluded that the apparently sigmoidal population growth was real. **Key words: wild sheep, temperature, census**

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_____, P. J. P. Gogan, J. M. Vore, and L. R. Irby. 2007. A simple solar radiation index for wildlife habitat studies. Journal of Wildlife Management 71(4):1344-1348. Abstract: Solar radiation is a potentially important covariate in many wildlife habitat studies, but it is typically addressed only indirectly, using problematic surrogates like aspect or hillshade. We devised a simple solar radiation index (SRI) that combines readily available information about aspect, slope, and latitude. Our SRI is proportional to the amount of extraterrestrial solar radiation theoretically striking an arbitrarily oriented surface during the hour surrounding solar noon on the equinox. Because it derives from first geometric principles and is linearly distributed, SRI offers clear advantages over aspect-based surrogates. The SRI also is superior to hillshade, which we found to be sometimes imprecise and ill-behaved. To illustrate application of our SRI, we assessed niche separation among 3 ungulate species along a single environmental axis, solar radiation, on the northern Yellowstone winter range. We detected no difference between the niches occupied by bighorn sheep (*Ovis canadensis*) and elk (*Cervus elaphus*; P=0.104), but found that mule deer (*Odocoileus hemionus*) tended to use areas receiving more solar radiation than either of the other species (*P*<0.001). Overall, our SRI provides a useful metric that can reduce noise, improve interpretability, and increase parsimony in wildlife habitat models containing a solar radiation component. **Key words: index, solar radiation, mule deer, bighorn, elk**

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Keay, J. A. and J. M. Peek. 1980. Relationships between fires and winter habitat of deer in Idaho. Journal of Wildlife Management 44(2):372-380. Abstract: White-tailed deer (*Odocoileus virginianus*) preferred unburned Douglas-fir (*Pseudotsuga menziesii*)/ninebark (*Physocarpus malvaceus*) habitat types in winter, except during February, when the unburned bluebunch wheatgrass (*Agropyron spicatum*)/bluegrass (*Poa sandbergii*) habitat type was preferred. Mule deer (*O. hemionus*) preferred burned Douglas-fir/ninebark and ponderosa pine (*Pinus ponderosa*)/bluebunch wheatgrass habitat types. White-tailed deer preferred sites that had the shortest average distance to cover, whereas mule deer selected sites that had significantly less cover. Relatively unpalatable species, including ninebark, were eaten more frequently on burned sites than on unburned sites. **Key words: mule deer, white-tailed deer, fire, habitat use**

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Kelsall, J. P. and W. Prescott. 1971. Moose and deer behaviour in snow. Canadian Wildlife Service Report, Series 15. A study of snow characteristics in relation to moose and deer behaviour in Fundy National Park. In three winters, there was 45% less snow under forest canopies than in the open. Snow was always deeper on moose range than on deer range. Deer avoided open areas, unless windblown, and where depths exceeded 40 cm, favoured well-established trails. Only a few large bucks remained at higher elevations. Travelling moose remained under forest canopies; this tendency increased with increasing snow depths. At depths > 97 cm, moose were rarely seen except in the trees. It is suggested that 70 cm is a critical snow depth for moose in Fundy National Park due to poor browse conditions. Moose and deer sink about equally far into snow of different densities but deer are more easily impeded because of their

smaller chest heights. Snow hardnesses were almost always lower under the canopy than in the open. Fewer crusts were found on deer range; probably as a function of lower elevation. It was difficult to reconcile the theory of ungulate support by snow crusts with available data. Crusts were rarely consistent enough to permit unhindered travel. Track depths for both moose and deer were consistently greater by a factor of 25—76% in the open than under the canopy. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver, BC, Canada, pp. 33-34.) **Key words: moose, white-tailed deer, snow, movement**

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Kirchhoff, M. D. and J. W. Schoen. 1987. Forest cover and snow: implications for deer habitat in southeast Alaska. Journal of Wildlife Management 51(1):28-33. Abstract: Relationships between snow depth and overstory characteristics were studied on 19 0.4-ha old-growth plots and 1 60-year-old 0.4-ha 2nd-growth plot near Juneau during winter, 1983-84. Mean tree diameter at breast height (dbh), number of stems/ha, percent Sitka spruce (*Picea sitchensis*), mean tree height, percent timber defect, basal area, and net timber volume were measured using variable plot and point-centered quarter techniques. Canopy cover was measured from photographs of the overstory taken at each snow measurement point. Snow depth in a high-volume plot (>100,000 board feet/ha) averaged 29% of that in an adjacent forest opening. Snow depth was correlated with net timber volume (r_s = -0.90), tree height (r_s = -0.85), basal area (r_s = -0.79), percent canopy cover (r_s= -0.76), percent spruce (r_s = -0.66), and mean tree diameter (r_s = -0.65). Old-growth plots with high net timber volume had the lowest snow depths. The low snow depths observed in high-volume, old-growth stands are attributed to the large-diameter limbs and deep crowns of older, dominant trees. Alaska Sitka black-tailed deer are at the northern limit of their natural distribution. Here, the ability of the forest overstory to intercept snow is critically important for deer winter survival. Winter track counts, pellet-group surveys, and radio-telemetry data show that low elevation, high-volume, old-growth stands are heavily used by deer during periods of deep snowfall. If deer are unable to leave high-volume winter range periodically because of adjacent clearcuts or unusually harsh winters, severe overbrowsing and range deterioration can result. **Key words: Sitka deer, snow, habitat use**

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Kjellander, P., J-M Gaillard, and A. J. M. Hewison. 2006. Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. Oecologia 146:521-530. Abstract: We investigated the influence of population density on juvenile body mass in two contrasting roe deer populations, in Sweden (Bogesund) and France (Chizé), in which density was monitored for ≥15 years. We investigated the effect of population density and climatic conditions on cohort performance. We predicted that: (1) body mass of growing fawns should be sensitive to environmental changes, showing marked between-year variation (i.e., cohort effects), (2) fawns in the less productive (weakly seasonal, weakly predictable summer weather) habitat of Chizé should show stronger density-dependent responses due to more severe food competition during summer than fawns in the more productive (markedly seasonal, moderately predictable summer weather) habitat of Bogesund, and (3) fawns at Bogesund should be heavier both in absolute terms and relative to their size than their

conspecifics in Chizé due to a higher degree of fat accumulation in northern environments. In both study sites we found marked cohort variation and clear effects of density, with body mass varying by as much as 29% over years. While neither summer nor winter climate influenced fawn body mass at Bogesund, fawns tended to be lighter after summers with high temperatures at Chizé. In addition, fawns were heavier after acorn mast years experienced *in utero* at Bogesund. As expected, the strength of the density-dependent response of fawn body mass was greater at Chizé than Bogesund. For a given density, male fawns were consistently heavier than females in both sites. Lastly, both sexes at Bogesund had higher absolute body mass and were larger for a given body size than in Chizé. Our results clearly demonstrate that absolute density is a poor predictor of roe deer performance and supports the view that habitat quality has an overwhelming importance for determining fawn body mass in roe deer populations. **Key words: roe deer, nutrition, morphology, temperature**

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Klein, D. R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. Journal of Wildlife Management 32(2):350-367. Abstract: Reindeer (*Rangifer tarandus*), introduced to St. Matthew Island in 1944, increased from 29 animals at that time to 6,000 in the summer of 1963, and underwent a crash die-off the following winter to less than 50 animals. In 1957 the body weight of the reindeer was found to exceed that of reindeer in domestic herds by 24-53 percent among females and 46-61 percent among males. The population also responded to the high quality and quantity of the forage on the island by increasing rapidly due to a high birth rate and low mortality. By 1963, the density of the reindeer on the island had reached 46.9 per square mile and ratios of fawns and yearlings to adult cows had dropped from 75 to 45 percent respectively, in 1957 to 60 and 26 percent in 1963. Average body weights had decreased from 1957 by 38 percent for adult females and 43 percent for adult males and were comparable to weights of reindeer in domestic herds. Lichens had been completely eliminated as a significant component of the winter diet. Sedges and grasses were expanding into sites previously occupied by lichens. In the late winter of 1963-64, in association with extreme snow accumulation, virtually the entire population of 6,000 reindeer died of starvation. With one known exception, all of the surviving reindeer (42 in 1966) were females. The pattern of reindeer population growth and die-off on St. Matthew Island has been observed on other island situations with introduced animals and is believed to be a product of the limited development of ecosystems and the associated deficiency of potential population-regulating factors on islands. Food supply, through its interaction with climatic factors, was the dominant population regulating mechanism for reindeer on St. Matthew Island. **Key words: caribou, nutrition, mortality, snow**

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_____, M. Meldgaard, and S. G. Fancy. 1987. Factors determining leg length in *Rangifer tarandus*. Journal of Mammalogy 68(3):642-655. Abstract: Leg length is quite variable within both domestic reindeer (*Rangifer tarandus* ssp.) and among the wild subspecies of *R. tarandus*, and appears to be under the control of several selective factors. These include nutritional constraints, the energetic efficiency of foraging through snow of various depths, the efficiency of locomotion where long migrations occur, and

fleetness related to predator avoidance. The net energy cost of walking or running a given distance on a hard surface decreases with increasing leg length, and the advantage of increased leg length in decreasing the cost of locomotion is even more pronounced in deep snow. However, the energetic advantages of long legs for movement in deep snow and for migration are counteracted by the energy costs to the animal for growth and maintenance of the additional tissues and possible decreased efficiency in foraging at or near ground level. The cline of decreasing leg length in *Rangifer* with increasing latitude is apparently the product of these selective mechanisms. This also seems to have been the case with the decreasing size of *Rangifer* during the Pleistocene and early Holocene. Evidence from domestic and feral reindeer, insular populations, and feeding experiments indicate that changes in nutrition can account for short-term changes in leg length in *Rangifer*, although these changes are usually allometric. This evidence is consistent with paleontological material from Greenland which also suggests that relatively rapid changes in body size (e.g., "dwarfism") may result from nutritional stress. **Key words: caribou, nutrition, snow, movement, morphology**

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Knight, M. H. 1995. Drought-related mortality of wildlife in the southern Kalahari and the role of man. African Journal of Ecology 33(4):377-394. Abstract: In the southern Kalahari during the dry season of 1985 varying numbers of ostrich and four large indigenous ungulate species died because of drought conditions. These dry conditions had prevailed for the previous six years. Percentage estimates of each population that died were: eland 35%, wildebeest 19%, red hartebeest 12%, gemsbok 1% and ostrich 10%. This die-off was unusual in that many eland, an intermediate feeder, succumbed to the dry conditions. This is contrary to the normal trend of large grazers suffering the greatest mortality. Mortality was least among adult females and yearlings that would have facilitated a rapid post-drought recovery of the populations. It is suggested that the dry season die-off of the migrant species (particularly wildebeest and eland) was exacerbated through the provision of artificial water-holes. This led to the attraction and concentration of animals in their summer season ranges during the dry winter. It is further suggested that poor-quality drinking water maybe increased mortality for several of the species. **Key words: drought, mortality, movement**

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Knight, R. R. 1970. The Sun River elk herd. Wildlife Monographs No. 23, The Wildlife Society, Washington, D.C. Abstract: During winter, the largest numbers of animals were observed on the Sun River Game Range. Numbers of animals using other parts of the winter range varied with severity of winter conditions. Use of vegetational types varied greatly among winters. Use of the grasslands averaged over the season ranged from 59% of the observed use in 1965 to 90% in 1962. This variation probably is best explained by differences in weather patterns and associated changes in migration patterns. In severe winters, large numbers of elk migrated down to the Sun River Game Range and thus were observed on the grasslands. Under moderate winter conditions, greater proportions of elk occupied the winter ranges in Sun River Canyon and relatively greater numbers were observed in Douglas-fir and on burns. During mild winters, percentages of elk observed on grasslands were great since greater numbers of elk

were able to spend the winter on transitional ranges where there were extensive grasslands.

Under exceptionally severe circumstances the elk used the timber in preference to grassland. A heavy snowfall early in February, followed by light thaw and a period of severe cold conditions, resulted in grassland areas being covered by a foot of snow with an overlying 0.75 inch of ice. The few animals observed on the grassland types at this time appeared to have difficulty in obtaining traction on the glazed crust. Most of the elk observed during this period were on the limber pine savannah where the crust did not form. Browse plants on bottoms were utilized during periods of general snow cover on the Sun River Game Range, since the snow was seldom deep enough to hinder elk movements.

Since more animals were observed on the Sun River Game Range in severe than in mild winters, it was assumed that the severity of the winter affected the habitual use of winter ranges. These changes were not interpreted as changes in winter home range, but a pattern of movement down the canyon in response to a more severe winter. **Key words: elk, snow, movement, habitat use**

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Kohler, J. and R. Aanes. 2004. Effect of winter snow and ground-icing on a Svalbard reindeer population: results of a simple snowpack model. Arctic, Antarctic and Alpine Research 36(3):333-341. Abstract. Winter climate is a key factor affecting population dynamics in high-arctic ungulates, with many studies showing a strong negative correlation of winter precipitation to fluctuations in population growth rate. Terrestrial ice crust or ground-ice can also have a catastrophic impact on populations, although it is rarely quantified. We assess the impact of winter climate on the population dynamics of an isolated herd of Svalbard reindeer near NyÅlesund with a retrospective analysis of past winter snowpack. We model landscape-scale snowpack and ground-ice thickness using basic temperature and precipitation data in a simple degree-day model containing four adjustable parameters. Parameter values are found that lead to model snow and ground-ice thicknesses which correlate well with three different model targets: reindeer population growth rates; April snow accumulation measurements on two local glaciers; and a limited number of ground-icing observations. We explain a significant percentage (80%) of the variance in the observed reindeer population growth rate using just the modeled mean winter ground-ice thickness in a simple regression. Adding other explanatory parameters, such as modeled mean winter snowpack thickness or previous years' population size, does not much improve the regression relation. **Key words: reindeer, snow, ice, model, population dynamics**

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Konjević, D., Z. Janicki, K. Severin, M. Stanko, T. Živičnjak, A. Slavica, and V. Starešina. 2007. An outbreak of tick paralysis in free-ranging mouflon (*Ovis ammon musimon*). Journal of Zoo and Wildlife Medicine 38(4):585-587. Abstract: An extremely warm autumn and prolonged warm weather conditions contributed to tick survival and might explain why this outbreak occurred in the middle of November. During November 2006, two live and one dead mouflon (*Ovis ammon musimon*) were presented with a history of weakness, tremors, and paralysis. After a detailed gross and histologic examination and a bacteriologic, parasitologic, and rabies evaluation, a

preliminary diagnosis of tick paralysis was established. A thorough field search revealed 13 affected mouflons found in the open hunting ground “Sveti Juraj” near the town of Senj (Croatia), along with an additional 35 mouflon carcasses. All 13 mouflons were placed in a quiet, semidark stable. All detectable ticks were removed manually, and the animals were topically treated with 250 ppm of Amitraz water emulsion (Taktic 12.5% EC, Intervet International, 5830 Boxmeer, Netherlands). The collected ticks were identified as *Ixodes ricinus, Dermacentor marginatus*, and *Haemaphysalis punctata.* In the following 24 hr, all treated animals recovered fully. This report describes a naturally occurring outbreak of tick paralysis in free-ranging mouflons from a karst habitat. **Key words: wild sheep, disease, temperature**

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Kudryashova, L. M. 1980. Effect of unfavorable weather conditions on female fecundity and survival of the young in the moose. Soviet Journal of Ecology 11(5):305-309. Abstract: The early and cold fall of 1976 in the Oka Reservation had a detrimental effect on the moose. Excessive cooling of females during this time was a factor in the resorbtion of some embryos. Further observations showed that the decrease in litter size during the embryonic period resulted in the birth of more viable offspring. Data are presented on the mortality of current-year young for two years. The winter of 1975/76 with heavy snowfall and the cool fall of 1976 were the most severe for the moose. **Key words: moose, snow, temperature, fecundity, mortality**

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Kumpula, J. and A. Colpaert. 2003. Effects of weather and snow conditions on reproduction and survival of semi-domesticated reindeer (*R. t. tarandus*). Polar Research 22(2):225-233. Abstract: In this work we investigated the effects of local weather and snow conditions on the reproduction and survival of semi-domesticated reindeer (*Rangifer t. tarandus*) from 1962 to 1987 in four separate study areas in northern Finland. Reindeer density had no negative effect on calf percentage in slaughter (October-January) in any area. The higher the number of very warm days or mean temperatures in summer, the lower was the calf percentage in all forested areas (Sodankylä, Muonio and Ivalo). In the Muonio area, calf percentage was also reduced by winters with abundant snow accumulation. In the open, mountainous Kevo area, calf percentage was reduced with a high number of warm days (mean T>0°C) during the previous December. However, if the previous May was warm in that area, it had an opposite effect. High reindeer densities seemed to increase mortality only in the Sodankyiä area. Abundant snow accumulation during winter reduced the survival index of reindeer both in the Sodankyiä and Ivalo areas. In the Muonio area, mortality of reindeer was increased with a high number of warm days in December. In the Kevo area, reindeer density or any climatic parameters could not explain yearly differences in mortality. This study indicated that permanent changes in climatic conditions could have different impacts in woodland as opposed to open, mountainous regions. In general, if global climatic change means weather instability in early winter and more snow, it also brings more difficulties for reindeer. However, if climate change means that snow melts earlier in the spring, some conditions could become more favourable tor reindeer. **Key words: reindeer, snow, temperature, fecundity**

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Kunkel, K. E., D. H. Pletscher, D. K. Boyd, R. R. Ream, and M. W. Fairchild. 2004. Factors correlated with foraging behavior of wolves in and near Glacier National Park, Montana. Journal of Wildlife Management 68(1):167-178. Abstract: We examined prey selection, search distance (measured as km traveled/kill), and spatial use of recolonizing wolves (*Canis lupus*) in a multi-prey system in northwestern Montana, USA, and southeastern British Columbia, Canada, from 1986 to 1996. Our objective was to explore factors affecting these parameters to better understand wolf-prey relationships of recolonizing wolves. Within white-tailed deer (*Odocoileus virginianus*) winter ranges, wolves selectively killed elk (*Cervus elaphus*) over deer. Number of wolves (r=0.67, P=0.03), year (r=0.68, P=0.02), and possibly human hunter-days/elk harvested (r=0.55, P=0.08) were positively correlated with variation in proportion of deer killed by wolves annually. Outside of severe winters, white-tailed deer, elk, and moose (*Alces alces*) appeared to be equally vulnerable to wolf predation. Search distance of wolves varied by up to 12 times annually. Snow depth (r=0.73, P=0.03) and proportion of total kills by wolves that were deer (r=0.66, P=0.06) were negatively correlated with the annual variation in the total search distance of wolves. Search distance per wolf were negatively correlated with the annual variation in the total search distance of wolves. Search distance per wolf was correlated negatively with year (r=0.66, P=0.06) and exponentially with hunter-days/elk harvested (r=0.70, P=0.04). Space use by wolves may have been in response to local changes in deer abundance. Wolves appeared to select the most profitable prey species. Severe winters and wolf selection for deer, coinciding with a decrease in elk numbers, increased wolf hunting efficiency by reducing search distance. Further research is needed to determine whether reduced search distance equates to increased kill rates by wolves in this system. Based on the time, expense, and difficulty of gathering data on wolf search distance in this system, however, we recommend against assessing impacts of wolves on prey via measuring kill rate. Rather, we suggest monitoring impacts of recolonizing wolves by directly assessing cause-specific mortality and recruitment rates of prey species. **Key words: elk, white-tailed deer, snow, predation**

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Labisky, R. F., K. E. Miller, and C. S. Hartless. 1999. Effect of Hurricane Andrew on Survival and movements of white-tailed deer in the Everglades. Journal of Wildlife Management 63(3):872-879. Abstract: Movements and survival of 32 radiomarked white-tailed deer (*Odocoileus virginianus seminolus*) were studied in the wet prairie of Everglades National Park (ENP) and Big Cypress National Preserve (BCNP) before and after the passage of Hurricane Andrew, a storm with sustained winds of 242 km/hr that bisected the study area on 24 August 1992. All radiomarked deer survived the hurricane. However, the hurricane, which struck during rut, appeared to reduce conception rates or fetus and fawn survival, or both, as evidenced by a 13-fold decrease in fawn production in 1993. Home range sizes, measured during January-March, did not differ ($P > 0.05$) among the years 1991, 1992 (prehurricane), and 1993 (posthurricane). Strong site fidelity in the wake of Hurricane Andrew was evidenced by the lack of difference ($P > 0.05$) in the distances between home range centers in prehurricane years (1991-92) and in pre- and posthurricane years (1992-93). Multiple response permutation procedure (MRPP) analyses revealed that although many deer altered ($P < 0.05$) their home range

use distributions between 1992 (prehurricane) and 1993 (posthurricane), these changes were consistent with those observed in the same deer between 1991 and 1992 (prehurricane years). In the absence of extraordinary or prolonged rainfall, hurricanes appear not to exert direct detrimental effects on deer populations in the interior marshes of the Everglades, but they may depress productivity of an annual cycle. **Key words: white-tailed deer, wind, productivity, movement**

177

Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology 65:653-670. Summary: 1. Density-independent weather effects can have important consequences for the demography of terrestrial herbivores because precipitation, temperature and insolation influence plant phenology, forage quality and biomass production, which in turn affects the habitat carrying capacity. Since forage digestibility influences intake and weight gain, life-history traits of young, growing animals are likely to reflect variation in the prevailing weather. 2. This paper specifically investigates spatial and temporal variation in age at maturation in female red deer (*Cervus elaphus*) in Norway in relation to climate variables known to influence primary production. Our findings are corroborated by analyzing differences in age at maturation in 21 cohorts of red deer on the Isle of Rum, Scotland. 3. In Norway the majority of females ovulated as yearlings and calved for the first time as 2-year-olds. The proportion calving for the first time at two years varied from 0·23 to 0·67 between regions and fluctuated from 0·46 to 0·76 between cohorts. On Rum, where age of maturation was delayed at least a year, the proportion calving for the first time as 3-year-olds varied between cohorts from 0·0 to 0·89. 4. In a subset of yearlings culled in Norway at the time of conception, the spatial and temporal differences in ovulation rates were related to the geographical and annual variation in body weight. 5. Both the spatial and temporal variation in the proportion of 2-year-olds calving in Norway, the cohort differences in the proportion calving as 3-year-olds on Rum, were negatively related to variation in May-June degree days 12 months earlier. 6. Although primary production on the preferred herb-rich *Agrostis-Festuca* grasslands was positively correlated with temperature in May and June on Rum, the proportion of females calving as three year old, was negatively correlated with annual differences in May-June primary production. 7. We argue that retarded phenological development, during periods of cooler weather, enhances diet quality because leaf:stem ratios and digestibility of plant parts decline more slowly. Thus, weight gain during the early summer growth spurt should be rapid during cool May-June weather, increasing the probability of conception in the autumn. 8. Since density-independent variation in food availability also influences fitness components which commonly have a more pronounced influence on population demography, for example offspring survival, we argue that our results highlight the potential importance of variation in weather on herbivore abundance. **Key words: diet, red deer, fecundity**

178

Larter, N. C and J. A. Nagy. 2001. Calf production, calf survival, and recruitment of muskoxen on Banks Island during a period of changing population density from 1986-99. Arctic 54(4):394-46. Abstract: Population estimates for muskoxen (*Ovibos moschatus*) (age >1 year) on Banks Island increased from 29,168 (SE 2104) n 1985 to a

peak of 64,608 (SE 2009) in 1994 and then declined to 45,833 (SE 1938) in 1998. From 1986 to 1999, annual sex and age classification surveys of muskoxen were conducted during summer. We estimated calf production (number of calves per 100 females aged 2 years or more), calf survival, and recruitment (number of yearlings per 100 females aged 2 years or more). Calf production ranged from 31.3 to 56.3 and was similar between periods of increasing and decreasing density (mean = 42.3 vs. 40.8). Calf survival ranged from 23% to 83% and was generally higher while density was increasing than during its decline (mean = 60 vs. 45). Survival at a given density was lower following the 1994 peak in density. Recruitment ranged from 10.0 to 41.7 and was higher (p = 0.06) during the period of increasing density than during the decline (mean = 28.0 vs. 17.2). Calf survival and recruitment were lowest following two consecutive severe winters, but animal density explained more of the variation in survival and recruitment than did late-winter snow depth. There was a positive relationship between the proportion of sedge (*Carex* spp., *Eriophorum scheuchzeri*) in the summer diet and calf survival and recruitment. Patterns of calf survival and recruitment plotted against density were consistent with those modeling a density-dependent relationship. Our results suggest that severe weather alone cannot explain the fluctuations in the population dynamics of Banks Island muskoxen and that underlying density-dependent responses acting upon calf survival and recruitment offer an alternative explanation. **Key words: muskoxen, snow, population dynamics**

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Laundré, J. W., L. Hernández, and S. G. Clark. 2006. Impact of puma predation on the decline and recovery of a mule deer population in southeastern Idaho. Canadian Journal of Zoology 84:1555-1565. Abstract: We modeled the impact of puma (*Puma concolor* (L., 1771)) predation on the decline and recovery of mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) in southern Idaho based on estimates of puma numbers, predation rates of pumas, and reproductive variables of deer. Deer populations peaked in 1992-1993, then declined more than 55% and remained low for the next 11 years. Puma numbers peaked 4-6 years after deer populations peaked but then declined to original levels. Estimated puma predation on the deer population before and after the decline was 2.2%-3.3%, and 3.1%-5.8%, respectively. At high puma densities (>3 pumas/100 km^2), predation by pumas delayed deer recovery by 2-3 years. Percent winter mortality of fawns (r^2+0.62, P<0.001) correlated positively with December-January snowfall. Incorporation of winter snowfall amounts in the model produced a pattern of deer population change matching estimated changes based on field survey data. We conclude that pumas probably were a minor factor in the decline of the deer population in our area and did not suppress deer recovery. We propose that winter snowfall was the primary ultimate and proximate factor in the deer decline and suppression of their recovery. **Key words: mule deer, snow, population dynamics, predation**

180

Lawrence, R. K., S. Demarais, R. A. Relyea, S. P. Haskell, W. B. Ballard, and T. L. Clark. 2004. Desert mule deer survival in southwest Texas. Journal of Wildlife Management 68(3):561-569. We studied population structure and limiting factors within a desert mule deer (*Odocoileus hemionus eremicus*) population in Brewster County of

the Trans-Pecos Region in Texas, USA. We estimated and compared annual survival and pregnancy rates from March 1990-February 1993 for 121 adults (>33 months old) male and female, 61 subadult (21-33 months old), and 77 young (8-20 months old) deer. Variation in weather patterns (i.e., drought) was associated with—if not causative of—annual variation in survival patterns. Adult female and young survival had the strongest correlation with drought. Pregnancy status of young (≤1.5 yr) and old (≥6.5 yr) deer appeared most affected by drought. Seasonal periods of natural stress differed for adult sex classes, with most female mortalities occurring during month associated with parturition and lactation, and most male natural stress losses occurring during the late winter and early spring. The major mortality sources were hunting and natural stressors for adult males, natural stressors and predation for adult females, and predation and natural stressors for young. Subadult mortalities were too few to identify significant mortality agents. The significance of natural stress-related survival and fecundity impacting herd productivity and stability warrants further consideration of poorly understood causative mechanisms. Ideally, replicated treatment areas would be used to address compensatory and additive mortality issues relative to predator abundance, harvest, and natural-stress losses. **Key words: mule deer, drought, mortality, fecundity**

181

Leckenby, D. A. 1977. Management of mule deer and their habitat: applying concepts of behavior, physiology and microclimate. Proceedings of the 4th Western Association of Fish and Wildlife Agencies and the Western Division, American Fisheries Society 57:206-217. Summary: Leckenby states the important facts can best be obtained by direct observation of mule deer interacting with their environment. He found subpopulations of Oregon mule deer moved within their home range according to weather severity, cover quality and forage availability. Thermal stress in winter makes cover of paramount importance in thermoregulation. Wind magnifies the effect several fold. Thermal stress in winter reduces the energy available for immediate survival and future production. Thermal stress from warm to cool weather during summer requires more energy for thermoregulation and is an extra maintenance cost for keeping deer cool or warm when cover is inadequate. Thermal stress in summer subtracts energy from immediate production and future survival. Microclimates play an important role and is the product of vegetation height, canopy closure, canopy depth and stem density. These components of plant community structure modify temperature, wind and radiation level. He cites research that show forest can reduce monthly maximum air temperature in the summer by about 10°F below that in the open, reduce annual rainfall through interception by 15 to 30%, and reduce wind velocities by 20-60%. Leckenby found that weather severity was 40% lower in a juniper stand than in adjacent shrubland. Thermal cover offered by juniper woodlands was intensively used during period of greatest thermal stress; shrublands were occupied most intensively when weather severity was moderate and forage was not available in grasslands; open grassland communities were mostly used when weather severity was least and phenologically young forage was most available. **Key words: mule deer, habitat use, behavior, thermoregulation, temperature, wind, topography**

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_____ **and A. W. Adams. 1986. A weather severity index on a mule deer winter range. Journal of Range Management 39(3):244-248.** Abstract: Temperature, wind, and snow conditions predictably affect the nutrition, behavior, distribution, productivity, and mortality of free-ranging cattle and big game in winter. Indexing of data obtained with commonly available weather instruments to reflect episodes of positive and negative energy balances of free-ranging ruminants could aid scheduling of feeding programs and planning of cover-forage manipulations. Such a weather severity index was developed and tested over 11 winters. Plausible levels of stress and episodes of relative severity were depicted during winters when mule deer exhibited low, moderate, and high mortality. The index curves mirrored over-winter declines of fat reserves probably sustained by mule deer. Lesser weather severity was predicted and measured in a western juniper woodland than in an adjacent rabbitbrush steppe community in southcentral Oregon. **Key words: mule deer, index, mortality**

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Leege, T. A. and W. O. Hickey. 1977. Elk-snow-habitat relationships in the Pete King Drainage, Idaho. Idaho Department of Fish and Game, Wildlife Bulletin 6. In Idaho, 93% of elk were concentrated on 27% of a drainage where snow was less than 61 cm deep. Snow depths were greatest on north aspects and less under mature trees than in brushfields. Not seen – cited in McLellan 1978. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography,* University of BC, Vancouver, BC, Canada, p. 34.) **Key words: elk, snow, distribution**

184

Lenart, E. A., R. T. Bowyer, J. Ver Hoef, and R. W. Ruess. 2002. Climate change and caribou: effects of summer weather on forage. Canadian Journal of Zoology 80:664-678. Abstract: In 1989, the Chisana caribou (*Rangifer tarandus*) herd in the northern Wrangell Mountains, Alaska, U.S.A., declined substantially in population size and productivity. Grasses, sedges, forbs, and willows (*Salix* spp.) are critical components of the diet of caribou in spring and summer, and the abundance and quality of forage are influenced by climate. To evaluate effects of climatic variation on caribou forage we conducted a field experiment in subarctic tundra where light, air temperature, and precipitation were manipulated. We used a plastic tarpaulin to increase air temperature and decrease precipitation. We also decreased light intensity with a shade cloth and increased precipitation by adding water to determine climatic effects on nutrient content and biomass of forage for caribou during the summers of 1994 and 1995. The most notable treatment effect on aboveground biomass was that shading resulted in higher nitrogen concentrations in all plant growth forms. In addition, shading consistently reduced biomass in forbs during mid and late season. Water treatment increased total plant biomass in the greenhouse plots during midseason in 1994 and in late spring in 1995. Water treatment also increased late-season biomass in control plots during 1994 but had no effect on biomass in shaded plots in either 1994 or 1995. A decline in nitrogen concentration in plants occurred throughout summer, a pattern that was not evident in *in vitro* dry matter digestibility. Climate variation and subsequent effects on forage plants have the potential to influence the population dynamics of

caribou through effects on their food supply. **Key words: caribou, temperature, precipitation, forage quality**

185

Lentz, C. P. and J. S. Hart. 1960. The effect of wind and moisture on heat loss through the fur of newborn caribou. Canadian Journal of Zoology 38(4):679-687. Abstract: The effects of air velocity and direction and of wetness on rate of heat transfer were studied in tests with samples of fur from five caribou calves. The rate of heat transfer through this fur increased by a factor of two to three with increase in air velocity from a negligible level (natural convection) to 23 m/second (direction parallel to sample). The effect of air velocity varied markedly (up to ±50% at 23 m/second) with inclination of the sample to the direction of air movement. Spraying water on the fur increased its rate of heat transfer markedly; addition of water equivalent to 10-12% of the volume of the fur doubled the rate of heat transfer. Other factors, such as erectness of the fur, direction of the hairs or "grain" of the fur with respect to the direction of air movement, and wetness of the skin also affected heat transfer. Differences between samples were large and did not appear to depend directly on the physical characteristics measured. **Key words: bioenergetics, wind, humidity, caribou**

186

Leopold, B. D. and P. R. Krausman. 1991. Factors influencing desert mule deer distribution and productivity in southwestern Texas. Southwestern Naturalist 36(1):67-74. Abstract: We assessed the distribution of desert mule deer (*Odocoileus hemionus crooki*) relative to abundance of plant species in Big Bend National Park (BBNP), Texas, from June 1972 to December 1981. We also evaluated the relation of spring rainfall on the percentage of fawns in the herd. We correlated relative deer abundance with plant, forage, and succulent plant (*Cactacae* and *Agave* sp.) densities. Differences in percentage fawns in the herd were related to spring rainfall and were attributed to the nutritional plane of reproducing does. Spring droughts are common in BBNP and contribute to maintaining numbers of deer at or below carrying capacity when predation by mountain lions (*Felis concolor*) is significant. Distribution and productivity of desert mule deer inhabiting arid environments may be significantly influenced by density-independent factors including plant density and rainfall. **Key words: mule deer, precipitation, fecundity, nutrition**

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_____ and _____.1987. Diurnal activity patterns of desert mule deer in relation to temperature. Texas Journal of Science 39(1):49-53. Abstract: Desert mule deer (*Odocoileus hemionus crooki*) activity in relation to temperature was studied in Big Bend National Park, Texas. No significant decrease in activity resulting from high temperatures occurred during spring and winter. Summer, and to a lesser extent late summer, activity significantly decreased when air temperature exceeded 33°C. Contrasting the activity patterns of desert mule deer with those of deer studied in more temperate regions, we found that the frequency of deer activity decreased when ambient temperatures reached deer body temperatures. Our observations support our initial hypothesis that observed activity patterns are a behavioral mechanism to avoid

temperatures that may result in thermoregulatory stress. However, we realize that measuring temperature without also considering thermal radiation and wind is simplistic in design. Further study is needed to assess these activity patterns in a more comprehensive manner. **Key words: mule deer, temperature, behavior, thermoregulation**

188

Lima, M. and A. Berryman. 2006. Predicting nonlinear and non-additive effects of climate: the Alpine ibex revisited. Climate Research 32:129-135. Abstract: Climate can have complex effects on demographic rates and the endogenous feedback structure regulating mammal populations, and this can create problems for predictive modeling. In northern and Alpine environments, weather appears to influence ungulate population growth rates mainly during years of high population density, suggesting the possibility of nonlinear interactions between the 2 variables. Threshold models have been employed to account for these nonlinearities. For example, in the case of Alpine ibex *Capra ibex* in the Gran Paradiso National Park of Italy, stronger density dependence is assumed to occur after snowfall exceeds 1.54 m. In this paper we use more objective nonparametric methods to evaluate the form of the functional relationships governing the dynamics of this ibex population. No evidence was found for a threshold effect in the data. Instead we uncovered a non-additive and nonlinear interaction between climate and population density. The resulting models predict ibex numbers as well or better than previous threshold models despite requiring fewer parameters, and also conform well to traditional ecological concepts. We conclude with several lessons for those who wish to predict the effects of climate change on animal population dynamics. **Key words: ibex, model, population dynamics**

189

Loe, L. E., C. Bonenfant, R. Langvatn, A. Mysterud, V. Veiberg, and N. Chr. Stenseth. 2006. Increased effect of harsh climate in red deer with a poor set of teeth. Oecologia 147:24-30. Abstract: Teeth are vital for mammal performance and especially in ungulates relying on mechanical decomposition of plant material for effective microbial digestion and energy uptake. The main focus of the role of teeth in ungulate life histories has been on tooth wear, while no one has addressed to what extent deviation from the natural set of teeth (maldentition) causes variation in individual fitness components. Based on mandibles from 41,066 individual red deer (*Cervus elaphus* L.) collected from 1969 to 2001, we tested whether maldentition had an effect on individual body condition and whether this effect depended on environmental harshness. Females with maldentition (0.6% of the population) were in a poorer condition than individuals without tooth anomalies and the effect increased during unfavorable climatic conditions. The effect of maldentition in males was less clear. This study indicates that a well-functioning set of teeth is essential for mammal performance, and that selection pressure against (dental) anomalies is more pronounced when climate is unfavorable. **Key words: red deer, NAO, mortality**

190

Loison, A. and R. Langvatn. 1998. Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. Oecologia 116:489-500. Abstract: Populations of red deer (*Cervus elaphus*) in Norway have increased continuously over the last decades. We tested the possible effects of climate and increase in population size on the survival rates and body condition of individuals in one of the northernmost populations of red deer in Europe. Based on 678 individuals of known age marked between 1977 and 1995, we estimated annual survival rates, the probabilities of being harvested and the recapture probability according to sex, age, year, winter and spring weather, population size, and, body weight and body condition, using capture-mark-recapture models. Winter harshness negatively influenced the body weight of yearlings and the survival of calves of both sexes. Spring weather influenced the survival of males in all age classes. A negative trend during the study period was detected in body weight and condition of calves and yearlings, but not in any age- or sex- specific survival rates. No significant gender differences in mean survival were shown in any age class. Moreover, there was little (male) or no (female) detectable between-year variation in survival rates for yearlings and adults. Winter weather acts as a limiting factor on population growth through a short-term effect on first-year survival and a long-term effect on body weight. We discuss the surprising low sex differences in natural survival rates and the differential effects of winter harshness on body weight, body condition and survival in relation to life history characteristics of red deer. **Key words: red deer, mortality, population dynamics**

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_____, R. Langvatn, and E. J. Solberg. 1999. Body mass and winter mortality in red deer calves: disentangling sex and climate effects. Ecography 22:20-30. Abstract: Understanding population dynamics of large mammals requires studies of variation in the age and sex-specific demographic parameters over time and the factors causing this variation. Here, we have focused on the variation in body mass of 8- to 10-month-old red deer calves, in relation to climate and sex over a 20-year period (1977-1997). We investigated the relationship between body mass and over-winter mortality during 1985 and 1986 and thereby, the phenotypic selection on body mass. We found a high variability from year to year in calf body mass. Males were consistently heavier than females. No interaction between sex and year was detected. The body mass of individuals from the same cohort shot during the annual hunting season and snow depth in January each explained ca 20% of the variability in calf body mass. Body mass loss during winter did not differ between sexes, but increased with body mass and varied from year to year. The probability of surviving was strongly related to body mass in each sex. For a given body mass relative to the sex-specific mean, males had a lower probability of survival than females. Hence, males had to be 1 kg larger than their mean in order to achieve the same survival as average-sized females. Our results suggested a directional phenotypic selection on body mass that led to an increasing body mass dimorphism in calves. The strength of this selection and the sex difference in the shape of the selection curve may depend, however, on the severity of winter and on sexual dimorphism in body mass at the beginning of winter. **Key words: mortality, red deer**

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Lomas, L. A. and L. C. Bender. 2007. Survival and cause-specific mortality of neonatal mule deer fawns, north-central New Mexico. Journal of Wildlife Management 71(3):884-894. Abstract: Because of significant declines in mule deer *(Odocoileus hemionus)* populations across New Mexico, USA, we investigated survival of fawns in north-central New Mexico, USA. We captured 19 fawns, 34 fawns, and 47 fawns in 2002, 2003, and 2004, respectively, and used fawn morphological measurements, habitat characteristics, and adult female (hereafter "female") condition to model preweaning fawn survival. Survival was 0.0, 0.12, 0.52 for 2002, 2003, and 2004, respectively, and was related to birth mass (X_1^2=9.5, *P*=0.002), birth date (X_1^2=8.4, *P*=0.004), litter size (X_2^2=9.4, *P*=0.009), female body fat (X_1^2=40.9, P,0.001), annual precipitation (X_1^2=35.0, P,0.001), summer precipitation (X_1^2=37.5, P,0.001),and winter precipitation (X_1^2=32.0, P,0.001).Total ingesta-free body fat of females (β=3.01, SE=0.75; odds ratio =20.19, 95% CI=4.64-87.91) and birth mass of fawns (β=1.188, SE=0.428; odds ratio = 3.38, 95% CI=1.42-7.59) were the best predictors of survival of individual fawns, although few of the logistic models differed in model selection criteria. Fawn survival in north-central New Mexico was driven by an interaction of total and seasonal precipitation and its effect on plant production, consequential effects on female nutrition, and ultimately, fawn birth attributes. Habitat conditions were so poor throughout north-central New Mexico during 2002 and 2003 (and likely during other drought years) that, based upon birth attributes, few fawns could have survived regardless of proximate causes of mortality. In 2004, precipitation enhanced security cover, maternal body condition, birth attributes and, thus, survival of fawns. However, more habitat enhancements are needed to improve the nutritional quality of mule deer habitats in north-central New Mexico and further enhance maternal and fawn condition to recover mule deer populations in this region. **Key words: mule deer, precipitation, nutrition, mortality, drought**

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Lovaas, A. L., J. L. Egan, and R. R. Knight. 1966. Aerial counting of two Montana elk herds. Journal of Wildlife Management 30(2):364-369. Abstract: Repeated aerial counts of elk (*Cervus canadensis*) were made during three winters in the Gallatin elk range, a narrow mountain canyon, and during one winter in the Sun River elk range, which covers a broad mountain front. Wide discrepancies in the results, within and between years, influenced mainly by snow conditions, were encountered in both areas. It is believed not feasible to apply statistical methods or reliability standards to the count results, and they are considered useful chiefly for following population trends, if evaluated in the light of weather conditions. When sportsmen representatives were included with the counting crews they were made aware of the inherent unreliability of the technique, but the practice required supplementary counts and aircraft, greatly increasing costs. **Key words: elk, snow, census**

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Loveless, C. M. 1964. Some relationships between wintering mule deer and the physical environment. North American Wildlife Conference 29:415-431. Summary: Loveless reports on the biological responses of mule deer to physical aspects of the

winter range environment, including influences of light, temperature, wind and precipitation. Deer made intensive use of shrub, open timber and shrub-understory types which had the longest duration of direct sunlight and highest radiation indexes. On warm spring days (45°F and higher) deer avoided direct sunlight, moving repeatedly to remain in shadowed areas. The authors observed that deer responded noticeably to temperature fluctuations, especially sudden and sharp increases or decreases. Movements from season to season were associated with air temperature. The vegetative cover apparently affected air temperature to a certain extent. When atmospheric moisture is low and duration increases, deer activity declines; an increase in moisture is associated with increased activity. Deer were seldom observed during high winds and low temperatures combined. Depth of ground-surface snow induced the most response, resulting in decreased use and movement of deer to lower areas. Snow of 10-12 inches impeded deer movement, especially yearlings; depths of 20-24 inches precluded use, greatly hampering locomotion. Snow depth was probably the principal deterrent in winter to forage utilization by deer. Wind generally only influenced deer during very cold weather. At temperatures of 15°F and below with high wind (25 mph+), deer avoided exposed browse slopes. Wind velocities were affected to a considerable extent by vegetative cover. **Key words: mule deer, behavior, humidity, movement, precipitation, solar radiation, temperature, wind**

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Lubow, B. C. and B. L. Smith. 2004. Population dynamics of the Jackson elk herd. Journal of Wildlife Management 68(4):810-829. We fit data on elk (*Cervus elaphus*) population size and composition, survival rates measured from their first week of life, reported harvest, and local weather to a series of alternative population models of the elk herd in Jackson, Wyoming, USA, for the period 1980-2002. Data were corrected for biases in aerial survey visibility, misclassification of juveniles in ground surveys, and harvest reporting. The models included explanatory variables for sex, age, population size, weather, and autocorrection of survival rates in different periods. Using information-theoretic model selection, we identified the most strongly supported models and effects. Model complexity ranged from 12 to 70 fitted parameters, and the best supported model contained 25 parameters. We estimated annual natural survival (excluding harvest) of mature (≥ 1 yr) elk of 96.8% (SE=1.5%) for males and 97.2% (SE=2.2%) for females. Natality was 60.4 juveniles/100 mature females (SE=3.9 juveniles/100 mature females). Sex ratio at birth strongly favored females (45.8% males, SE=1.6%, Akaike weight=99.9%). The dynamics of this population were well explained by annual variation in survival of neonates (birth to 31 Jul), juvenile survival during late winter (20 Feb-19 May), and harvest. Survival of neonates was correlated with several weather covariates that apparently affected nutritional status of their mothers. Survival of juveniles during late winter was related to weather conditions during the preceding summer and early winter. We found a compensatory effect of juvenile harvest on subsequent juvenile survival in late winter; 89% of increased juvenile harvest was offset by reduced natural mortality. We also found evidence for a decline in survival of neonates with increasing population size (density dependence). However, the density effect was weak at current population size and recent supplemental feeding rates. Thus, only continued or increased female harvest can maintain this population at current or lower levels if current feeding policies are continued—unless disease prevalence, predator impacts, or other

factors substantially alter the historical dynamics. Simulations suggested that harvest rates of mature females must be increased to 15.1% from recent levels of 11.9% to reduce the current population of 15,680 elk (SE=407) to the target population size of 11,029 set by the Wyoming Game and Fish Department (WGFD). Sensitivity of equilibrium population size at the WGFD target level to harvest rate was very high, requiring regular monitoring and adjustment of harvest to maintain a stable population. **Key words: elk, nutrition, mortality**

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Lundmark, C. and J. P. Ball. 2008. Living in snowy environments: quantifying the influence of snow on moose behavior. Arctic, Antarctic and Alpine Research 40(1):111-118. Abstract: We investigated the effects of snow and environmental variables on the depths to which moose sank in snow, and the extent to which moose followed in the tracks of other free-ranging moose in the mountains of the sub-arctic areas of northernmost Sweden. We tested a method to combine the variables that affect snow quality (e.g. density and hardness) into a single variable that is easier to measure in the field. We also studied the snow conditions in the summer and winter ranges of migrating moose. First, we performed correlation analyses that revealed that sinking depths of moose decreased with increasing snow quality, snow depth, altitude, and air temperature. Next, we next used the Akaike information criterion (AIC) to determine the best model of sinking depth, which indicated that the important variables were snow quality, altitude, and snow temperature. For trail-following behavior, the best model included air temperature only. Regarding seasonal ranges, winter ranges had considerably less snow than the summer ranges that these individual moose left, but snow quality did not differ. Overall, our new method to index snow quality (here, using a dynamometer to measure the force required to press a simulated moose foot down in the snow to the depth of a moose footprint) shows promise, and we suggest that future studies of ungulate winter ecology investigate it further. **Key words: moose, snow, behavior, temperature, index**

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Lyon, L. J. 1979. Influences of logging and weather on elk distribution in western Montana. USDA Forest Service Research Paper INT-236, Intermountain Forest and Range Experiment Station, Ogden, Utah. Summary: Distributions of elk pellet groups on an area of 215 km^2 (80 mi^2) were examined for a period of 8 years. Recorded changes in annual distribution describe both elk movement in response to disturbances in the forest environment and elk habitat selection in response to weather conditions.

Over a period of years, the single most important influence on elk distribution in the Burdette Creek-Deer Creek area was weather. And, whereas the manager has no control over weather, there were at least three responses by elk that can be used by managers. There was fairly strong evidence that acceptable winter range may include more area than is usually considered in habitat improvement planning. In 4 of the 8 years of study, elk were able to spend a substantial part of the winter period above 1524 m (5,000 ft) on areas normally considered summer range. Increased forage production at this elevation is not as critical for elk as increases below 1372 m (4,500 ft) might be, but the benefits could be greater than is usually assumed.

Another important response by elk was the early movement to less accessible areas when snow fell during the hunting season. Normally, snow aids the hunter in tracking elk and thereby increases the annual harvest. If adequate refuge areas do not exist, over harvest is a distinct possibility.

Finally, the behavioral response of elk to hot, dry summer weather in 2 different years can be taken as further evidence of the importance of cool, moist habitat types to the overall integrity of elk summer ranges. Maintenance of body temperature at some relatively constant level may be comparable to feeding as a daily preoccupation of elk. **Key words: elk, distribution, movement, snow, behavior, temperature, thermoregulation**

198

McCulloch, Jr., C. Y. 1955. Utilization of winter browse on wilderness big game range. Journal of Wildlife Management 19(2):206-215. Summary: Late in December, 1951, unusually heavy wet snow fell steadily for several days. This snow clung to the browse plants, bending and burying many of them. Subsequent snowstorms buried these plants even more deeply, and a heavy crust eventually formed on the snow. Regardless of its height, much browse was made unavailable during the greater part of the winter. Some browse forage is made unavailable every winter by snow, but these conditions were unusually severe during the winter of 1951-52. Palatable plants which were unavailable during this particular winter nevertheless showed a generally hedged and severely overused condition, attesting to their availability during previous winters. The deep snows of the winter of 1951-52 caused elk to concentrate in the bottom and adjacent lower slopes of the Selway canyon, resulting in high utilization of the principal browse species. Also, the effect of the open winter of 1952-53 is seen in the comparatively light use of the same species. **Key words: elk, snow, ice, temperature, nutrition, forage quality, movement**

199

McCullough, D. R. 1964. Relationship of weather to migratory movements of black-tailed deer. Ecology 45(2):249-256. Abstract: A study of the influence of weather factors on the migrations of a herd of black-tailed deer showed that periods of migration as indicated by night spotlight samples were closely correlated with seasonal changes in minimal relative humidity. Both spring and fall migrations, and possibly an atypical summer movement, occurred during ranges of 40 to 60% minimal relative humidity. Snowstorms, rainfall, absolute humidity, and temperature were not so closely correlated. The migrations could not be attributed to habitat factors such as food, water, or escape cover. **Key words: black-tailed deer, migration, humidity, snow, precipitation, temperature**

200

McDaniel, C. S. 2002. Lamb production and survival of a bighorn sheep population in central Idaho. Proceedings Northern Wild Sheep and Goat Council 13: 221. Abstract (Only): Long-term monitoring allows for the establishment of baseline data over extended time periods and gives biologists the opportunity to quantify data into predictive management strategies. The Rocky Mountain bighorn sheep (*Ovis*

canadensis) population in the Big Creek drainage of the Frank Church-River of No Return Wilderness in central Idaho experienced a sudden population decline from 1988 to 1990 as a result of a *Pasturella* related die-off. Extensive monitoring of the population during that period provided information on lamb production and survival during the die-off phase of a *Pasturella* die-off. A replicate survey of lamb production and survival was conducted during the summer of 2001 to assess the recovery stage of the die-off. The average number of lambs:100 ewes was established for three different lambing areas across three different time periods. These were compared to similar data collected during the summers of 1989 and 1990. Chi-square analysis of this data showed significant differences between total 1989-1990 ratios and 2001 ratios but not between lambing areas in each of the die-off and 2001 periods. Results show a high survival ratio through the beginning of August 2001 (avg. 86:100) compared with a significantly lower ratio in August 1989 (avg. 19:100) and August, 1990 (avg. 12:100). Thirteen years of lamb:ewe ratio data, collected between 1985 and 2000 were regressed against precipitation. Lamb recruitment through the following spring was positively correlated with March precipitation. **Key words: wild sheep, precipitation, recruitment, disease**

201

McDonald, C. G., S. Demarais, T. A. Campbell, H. F. Janssen, V. G. Allen, and A. M. Kelley. 2005. Physical and chemical characteristics of antlers and antler breakage in white-tailed deer. Southwestern Naturalist 50(3):356-362. Abstract: Previous descriptions of growth, development, and composition of deer antlers have not included factors that affect antler breakage. We related morphology and mineral concentration to occurrence of broken antler tines in white-tailed deer (*Odocoileus virginianus*) using 126 cast antlers collected during 1989 to 1995. Antler were divided into 2 categories: broken and intact. Density, break strength, spongy bone percentage, and mineral composition were measured for 1-cm cross-sections removed from the base of the main beam, from between the G2 and G3 tines, and from the base of the G3 tine. We compared these variables between broken and intact antlers and estimated correlations between tine density, break strength, spongy bone ratio, and mineral composition. Density, percentage of spongy bone, break strength, and mineral concentration did not differ significantly between broken and intact antlers. Main beam break strength differed significantly among years. Mineral composition differed significantly among antler locations and year. Rainfall during the antler growth period was correlated with concentrations of aluminum and manganese. Although there were significant correlations between morphology and mineral concentrations, morphology and mineral composition did not explain the presence of broken antlers. **Key words: white-tailed deer, antler, precipitation**

202

McGinnes, B. S. and R. L. Downing. 1977. Factors affecting the peak of white-tailed deer fawning in Virginia. Journal of Wildlife Management 41(4):715-719. Abstract: Birth dates of 503 white-tailed deer (*Odocoileus virginianus*) fawns captured during a 10-year period at Radford Army Ammunition Plant, Dublin, Virginia, were found to be earlier in those years when the does had reached estrus presumably in better condition. Years of early mean birth dates were significantly correlated with high rainfall the previous May and with a low fawn survival rate the previous summer. Rainfall and

snow cover during gestation and cloudiness and temperatures prior to conception were not significantly correlated with birth dates of fawns. **Key words: deer, parturition, precipitation, snow, temperature**

203

Mackie, R. J., D. F. Pac, K. L. Hamlin, and G. L. Dusek. 1998. Ecology and management of mule deer and white-tailed deer in Montana. Montana Department of Fish, Wildlife & Parks, Helena, Montana, USA. Notes: The authors state that in variable environments such as the timbered breaks and prairie-badlands of Montana, some summer maintenance habitat may become reproductive habitat in wet years and some reproductive habitat may become only maintenance habitat in dry years. Winter maintenance habitat for both mule deer and white-tailed deer in mountain environments was associated with areas receiving minimal snow accumulation brought about by geographic location, topography, vegetation and climate. In their study area drought with reduced snowfall typically increased the amount, if not the quality, of available winter maintenance habitat. Stands of coniferous timber and broken topography were important features enhancing energy conservation through specialized use of habitat, particularly in deep snow environments. Deer behavior varies based on the physical structure of their habitats. **Key words: mule deer, white-tailed deer, habitat use, snow, temperature, topography, nutrition, behavior**

204

McKinney, T. 2003. Precipitation, weather and mule deer. Pages 219-237 *in* deVos, Jr. J.C., M. R. Conover, and N. E. Headrick, Mule Deer Conservation: Issues and Management Strategies. Jack H. Berryman Institute Press, Utah State University, Logan. This chapter provides an overview of the research, conclusions and suggestions regarding the importance of precipitation and other weather variables in directly or indirectly affecting mule deer populations. Included are discussions on vegetation response to precipitation (or lack of it) and its impact on the diet and nutrition of mule deer and the carrying capacity of the range. The authors also discuss the impacts of precipitation on population dynamics, distribution and movement, predation, disease and management. **Key words: mule deer, precipitation, movement, predation, disease, population dynamics**

205

_____ and T. W. Smith 2007. Diets of adults and lambs of desert bighorn sheep during years of varying rainfall in central Arizona. Southwestern Naturalist 52(4):520-527. Abstract: Effects of unpredictable, variable rainfall in arid systems on diets of adults and lambs of desert bighorn sheep (*Ovis canadensis*) are poorly understood. We determined associations based on analysis of feces between amounts of rainfall and composition and similarity (overlap and diversity) of diets of adults and lambs, and relationships between diets of adults and lambs, in the Sonoran Desert of central Arizona during 1999-2003. Drought occurred in 2 of 3 years during sampling of feces of adults, and in 1 of 3 years during sampling of feces of lambs. Composition and diversity of diets of adults were comparable during years of drought and normal rainfall, except that diets were not correlated between years when severe drought (31% of long-

term average rainfall) followed normal rainfall. Composition and diversity of diets of lambs also were independent of amounts of rainfall, but dietary overlap between and within age groups was greater during years of increasing rainfall compared to previous years. We hypothesized that amounts of rainfall moderately influenced diets of adults and lambs of desert bighorn sheep, but diets generally were closely linked among years and between age classes, and associations tended to persist independently of amounts of rainfall. Improved quality of diets and higher production, particularly of forbs, were more important proximate factors than composition of diets in affecting differences in nutritional status of adults and lambs between drier and wetter years. Furthermore, selection of forage by lambs likely is learned, at least in part, through associations, particularly with their mothers, prior to weaning. **Key words: wild sheep, precipitation, drought, diet**

206

_____, T. W. Smith, and J. C. deVos, Jr. 2006. Evaluation of factors potentially influencing a desert bighorn sheep population. Wildlife Monographs 164:1-36.
Abstract: We studied a desert bighorn sheep (*Ovis canadensis*) population in the Mazatzal Mountains (primary study area) in central Arizona and population indices on reference areas between 1989 and 2003. We evaluated disease exposure and nutritional status of desert bighorn sheep, vegetation parameters, predator diets, and mountain lion (*Puma concolor*) harvest and abundance (1999-2003) and mountain lion predation (1995-2003) as factors potentially affecting desert bighorn sheep and population parameters. We measured rainfall monthly, monitored demography and relative abundance of desert bighorn sheep using aerial surveys, captured and placed radiocollars on desert bighorn sheep, and collected samples of blood, parasites, and other pathogenic agents from captured animals. We measured mineral content, relative use, and structural composition of vegetation and determined diets of desert bighorn sheep adults and lambs, dietary intakes of nitrogen (FN), 2,6-diaminopimelic acid (FDAPA), neutral detergent fiber, and minerals using fecal analyses. We incorporated mountain lion reductions as an experimental element, monitored harvest, and used track surveys as an index of relative abundance of the predator and monitored radio-collared desert bighorn sheep to determine mortalities and causes of death. We determined diets of bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and mountain lions using fecal analyses. Drought conditions occurred during summer (July-September) and winter (November-April) during 4 and 3 years, respectively, between 1999 and 2003. Annual surveys indicated that the Mazatzal Mountains population declined during drought between 1994 and 1997experienced low growth and lamb production coincident with above-normal rainfall in 1998 and drought in 1999, and exhibited higher growth, production, and productivity during 2000-2003 despite persistent drought conditions during this period. We observed no clinical symptoms of disease in radio-collared desert bighorn sheep, and hematological and other evidence of exposure to disease agents was unremarkable. Population indices on the primary study and reference areas were positively correlated with winter (November-April) rainfall. We found no evidence of forage overutilization on the primary study area. Rainfall on Mazatzal Mountains was associated with differences in primary production, particularly of forbs, forage mineral concentrations, and diets, nutritional status, and demographic attributes of desert bighorn sheep between 1999 and 2003. Higher winter rainfall was associated with higher

forb growth, and higher rainfall was associated with higher concentrations of P and Se but lower levels of Fe in browse; higher concentrations of Ca, P, and Zn in forbs; and higher levels of P, Se, and Zn in grasses. Narrower mean Ca:P ratios of browse and forbs were associated with higher rainfall. Diets of desert bighorn sheep adults and lambs generally were similar, particularly near summer, and forbs tended to predominate in diets during wetter and drier years. Higher winter rainfall was associated in adult feces with more prolonged winter-to-spring increases in FN and FDAPA concentrations, higher winter rainfall corresponded in lamb feces with higher levels of FN, FDAPA, and fecal P; lower concentrations of fecal Ca; and narrower fecal Ca:P ratios. Thus, we hypothesized that diets and nutritional status of desert bighorn sheep adults and lambs tended to correspond with rainfall patterns and associated differences in relative abundance and mineral content of forages. We found no evidence that bobcats or coyotes preyed on or scavenged desert bighorn sheep. Decline of desert bighorn sheep abundance during 1994-1997 was greater than declines on reference areas lacking mountain lions despite continually higher, and a lesser decline in, winter rainfall on the primary study area. In comparison, population indices on a reference area and on Mazatzal Mountains increased between 1999 and 2003 in association with predator reductions and lower abundance of mountain lions and predation of radio-collared animals despite continued occurrences of drought during this period. We thus identified 2 proximate factors that likely acted to influence demographic trends of the Mazatzal Mountains desert bighorn sheep population: nutritional status (higher rainfall[ultimate factor] was associated with higher availability and differences in mineral content of forages and improved indices of desert bighorn sheep nutritional status) and predation by mountain lions. We hypothesize that nutritional status and mountain lion predation during a period of drought influenced desert bighorn sheep population parameters in Mazatzal Mountains and that short-term removal of mountain lions by lethal harvest contributed to higher growth and productivity of the small, isolated population, even during periods of drought. **Key words: wild sheep, precipitation, drought, nutrition, predation**

207

_____, T. W. Smith, and J. D. Hanna. 2001. Precipitation and desert bighorn sheep in the Mazatzal Mountains, Arizona. Southwest Naturalist 46(3):345-353. Abstract: We examined demography of a population of desert bighorn sheep (*Ovis canadensis*) in the Mazatzal Mountains, Arizona, in association with annual and seasonal rainfall and relative herd density over an 11-year period that encompassed increasing, but normal median, annual precipitation (1989-1993) and drought conditions (post-1993). During wet years of 1989-1993 and through 1994, the population was stable or increasing slightly, and desert bighorn were distributed throughout the study area. Relative abundance of yearlings was positively correlated during wet years with total annual rainfall from the same year, and winter rainfall was positively correlated with number of groups observed 1.5 years later. In contrast, total males, Class I and II males, lambs observed per hour of survey time, and lambs:100 females declined during the post-1993 drought. Declining winter rainfall during drought was correlated with total desert bighorn female and yearling observations per hour, and with yearling recruitment 1.5 years later. We found no clear evidence suggesting density dependent effects on recruitment during wet or drought years. However, lower population densities during drought corresponded with a contraction of bighorn distribution. The proportion of Class IV males in the total

population of males was lower than expected throughout the study and was independent of rainfall. Our results indicate that annual and seasonal rainfalls are important variables driving the dynamics of bighorn sheep populations in desert environments. **Key words: wild sheep, precipitation, distribution, fecundity**

208

McRoberts, R. E., L. David Mech, and R. O. Peterson. 1995. The cumulative effect of consecutive winters' snow depth on moose and deer populations: a defense. Journal of Animal Ecology 64(1):131-135. Summary: 1. L. D. Mech *et al* presented evidence that moose *alces alces* and deer *Odocoileus virginianus* population parameters are influenced by a cumulative effect of three winters' snow depth. They postulated that snow depth affects adult ungulates cumulatively from winter to winter and results in measurable offspring effects after the third winter. 2. F. Messier challenged those findings and claimed that the population parameters studied were instead affected by ungulate density and wolf indexes. 3. This paper refutes Messier's claims by demonstrating that his results were an artifact of two methodological errors. The first was that, in his main analyses, Messier used only the first previous winter's snow depth rather than the sum of the previous three winters' snow depth, which was the primary point of Mech *et a*l. Secondly, Messier smoothed the ungulate population data, which removed 22-51% of the variability from the raw data. 4. When we repeated Messier's analyses on the raw data and using the sum of the previous three winter's snow depth, his findings did not hold up. **Key words: moose, deer, snow, predation**

209

Maier, J. A. and E. Post. 2001. Sex-specific dynamics of North American elk in relation to global climate. Alces 37(2):411-420. Abstract: The North Atlantic Oscillation (NAO) is a continuous fluctuation in atmospheric mass balance that drives most interannual and decadal variation in winter temperatures and precipitation in the Northern Hemisphere. Effects of the NAO on the population dynamics of red deer (*Cervus elaphus*) in northern Europe and white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) in North America are well documented. In northern Europe, analysis of sex-specific population dynamics in relation to the NAO have documented divergent responses of the sexes to winter warming, but such analyses have been lacking for North American ungulates. We investigated effects of the NAO on the sex-specific population dynamics of Roosevelt elk (*Cervus elaphus roosevelti*) on Raspberry Island, Alaska, USA. Density of females and of the total population declined after positive (cold and snowy) NAO winters. Density of males was unrelated to the NAO index. Production of young was limited by density of females and increased following positive NAO winters. Hence, in agreement with analyses of the dynamics of red deer in northern Europe, population dynamics of the herd on Raspberry Island related mainly to the influences of winter climate and density on abundance and productivity of females, rather than males. **Key words: elk, NAO, population dynamics, sex ratio, temperature, snow, productivity**

210

Mandujano, S. 2006. Preliminary evidence of the importance of ENSO in modifying food availability for white-tailed deer in a Mexican tropical dry forest. Biotropica 38(5):695-699. Abstract: The influence of El Niño/Southern Oscillation (ENSO) on rainfall and its possible effect on availability of food for white-tailed deer (*Odocoileus virginianus*) in a tropical dry forest in the Pacific coast of Mexico was studied. From 1977 to 2003 there were three significant El Niño and La Niña events. Dring El Niño years rainfall decreased during the wet season (June to October) and increased during the dry season (November to May), with the opposite effect during La Niña years. Plant diversity was monitored in permanent plots during the wet and dry seasons of 1989-1993. The results provide evidence that ENSO events affect deer food availability, particularly in the dry season. **Key words: precipitation, white-tailed deer, nutrition, ENSO, El Niño, La Niña**

211

Månsson, L., J. Ripa, and P. Lundberg. 2007. Time series modeling and trophic interactions: rainfall, vegetation and ungulate dynamics. Population Ecology 49:287-296. Abstract: Time series analysis is a tool that is now commonly used when analyzing the states of natural populations. This is a particularly complicated task for ungulates, since the data involved usually contain large observation errors and span short periods of time relative to the species' life expectancies. Here we develop a method that expands on previous analyses, combining statistical state space modeling with biological mechanistic modeling. This enables biological interpretability of the statistical parameters. We used this method to analyze African ungulate census data, and it revealed some clarifying patterns. The dynamics of one group of species were generally independent of density and strongly affected by rainfall, while the other species were governed by a delayed density dependence and were relatively unaffected by rainfall variability. Dry season rainfall was more influential than wet season rainfall, which can be interpreted as indicating that adult survival is more important than recruitment in governing ungulate dynamics. **Key words: model, populations dynamics, precipitation**

212

Marcum, C. L. and M. D. Scott. 1985. Influences of weather on elk use of spring-summer habitat. Journal of Wildlife Management 49(1):73-76. Summary: Marcum and Scott examined correlations between cumulative precipitation and summer temperatures with intensity of elk selection for a specific drainage and selection for elevation, aspect, overstory canopy, and plant community. August counts of pellet groups prior to logging activities indicated summer elk use of this study area during a drought year was 4.2 times the use during a wet year. High negative correlations were found between summer elk use of the study area and cumulative precipitation during the preceding October-August period. Cumulative precipitation in previous months was a better predictor of spring and summer elk use in the study area than was spring and summer precipitation alone. Correlations between elk use of the study area and monthly or seasonal precipitation were generally low and nonsignificant. Similarly, no significant correlations were found between annual elk use of the study area and mean daily

temperature. Percentage use of selected habitat components for five summers by radio-collared elk was correlated with mean daily temperatures for July-August and cumulative precipitation for October-August. Except for the wettest and coolest year, cool, moist habitat types and dense overstories were preferred. Annual precipitation was strongly correlated with elk use of warm, dry habitat types on open forest sites. Elk use of dense forest stands was positively correlated with mean daily July-August temperature. Yearly differences in elk distribution and habitat use are likely the result of direct and indirect weather influences. **Key words: elk, precipitation, temperature, habitat use**

213

Marsh, H. 1938. Pneumonia in Rocky Mountain Bighorn sheep. Journal of Mammalogy 19(2):214-219. The author describes instances of pneumonia in bighorn sheep of Montana in the 1920s and 1930s. On the northern Yellowstone range he noted that the habitat had been seriously damaged by dry weather and seriously overgrazed by sheep, antelope, deer and elk. Several of the sheep observed, including a lamb, were seen coughing after exertion. Marsh notes that the sheep observed moved down from high range early and were seen on their fall range as early as September. The winter range was not available due to land development and areas occupied in the fall were grazed all during the winter. In Yellowstone Park this fall and winter range area was heavily grazed by elk, deer, antelope and sheep. He notes that in some seasons the temperature is high enough in September to November to permit the completion of the life cycle of the lungworm through infested snails resulting in heavier infestation than if the bighorns had free access to sufficient fall and winter range. Also overgrazed and crowded range greatly increased opportunity for transmission of secondary bacterial invaders from sheep to sheep. He concludes that the lack of normal winter range, causing crowding and overgrazing on fall and spring range, combined with feeding in the case of Glacier Park sheep, were factors in the development of clinical parasitism and secondary bacterial pneumonia in the bighorns. **Key words; wild sheep, temperature, habitat use, disease, forage quality**

214

Marshal, J. P., P. R. Krausman, and V. C. Bleich. 2005. Rainfall, temperature, and forage dynamics affect nutritional quality of desert mule deer forage. Rangeland Ecology and Management 58(4):360-365. Abstract: Forage quality affects physiological condition, population dynamics, habitat use, and distribution of ungulates. We studied how rainfall, temperature, forage biomass, and forage growth are related to water content, crude protein (CP), and in vitro dry matter digestibility (IVDMD) of some common forage species of desert mule deer (*Odocoileus hemionus eremicus* Mearns) in the Sonoran Desert, California. We established vegetation transects in desert washes to collect forage samples and to measure forage biomass, growth, rainfall, and temperature on a quarterly basis. Percent water and CP were positively associated with forage growth (P<0.001) and with rainfall (P<0.025). There were positive relationships between IVDMD and forage growth (P<0.001), forage biomass (P<0.001), and the combination of temperature and rainfall (P<0.001). These findings suggest that the highest quality landscapes for deer are those with rapidly growing forage where forage water, CP, and IVDMD are greatest. With the quantified relationships between rainfall, temperature, and forage characteristics presented here, the nutritional constituents for deer forage can be

predicted. **Key words: mule deer, precipitation, temperature, forage quality, nutrition**

215

_____, _____, _____, W. B. Ballard, and J. S. McKeever. 2002. Rainfall, El Niño, and dynamics of mule deer in the Sonoran Desert, California. Journal of Wildlife Management 66(4):1283-1289. Abstract: We used long-term El Niño oscillation (ENSO), rainfall, and deer harvest records to investigate effects of ENSO and rainfall on mule deer (*Odocoileus hemionus*) population trends in the Sonoran Desert, southeastern California, USA. We found significant relationships between the southern oscillation index and rainfall (R^2=0.38, $P \leq$ 0.001), and between rainfall and annual deer harvest (R^2=0.25, $P \leq$0.001). We also found that deer harvest (i.e., an index of deer abundance) in any year was related to accumulations of rainfall >5 years before that hunting season (R^2=0.34), whereas the change in harvest between years (i.e., an index of rate of population change) was most related to rainfall the year immediately prior to that hunting season (R^2=0.15). Fluctuations in deer populations in the deserts of California ultimately may be caused by ENSO events. **Key words: mule deer, precipitation, population dynamics, harvest, El Niño, ENSO**

216

Martin, T. E. 2007. Climate correlates of 20 years of trophic changes in a high-elevation riparian system. Ecology 88(2):367-3280. Abstract: Snowfall can affect overwinter presence of elk, whose browsing can significantly impact deciduous tree abundance. Thus, climate may affect the plant community indirectly through effects on herbivores, but may also act directly by influencing water availability for plants. **Key words: elk, snow, vegetation**

217

Martinka, C. J. 1969. An incidence of mass elk drowning. Journal of Mammalogy 50(3):640-641. Notation: In this short piece, Martinka documents the drowning of a large number of elk near St. Mary Lake, Glacier National Park in February 1968. Forty elk carcasses were frozen in the lake 500 feet from shore. Exhaustion, exposure and drowning were considered the proximal causes of death. This event was preceded by unusual weather conditions including winds above 100 mph that disintegrated the ice cover; the water subsequently refroze into clear, smooth ice apparently weakened by temperatures as high as 55°F. During this period the herd had traveled onto the lake and broken through. A following dip in temperature to -16°F strengthened the ice, encapsulating the animals. At least 26 carcasses floated to shore from March through August. **Key words: elk, mortality, wind, temperature**

218

_____. 1967. Mortality of northern Montana pronghorns in a severe winter. Journal of Wildlife Management 31(1): 159-164. Abstract: Winter mortality of pronghorn antelopes (*Antilocapra americana*) was studied near Glasgow, Montana, in April, 1965. A minimum loss of 500 pronghorns was associated with severe weather and occurred primarily on foothill grassland along the Milk River. Bone marrow examination of 59

carcasses indicated that malnutrition was the principal cause of death. Sex and age composition of 327 carcasses was 28, 33, and 39 percent fawns, adult males, and adult females, respectively. Comparison of carcass age ratios with ratios observed in summer herds suggested a differentially high mortality for fawns but not for yearlings. A low mortality rate was indicated for 2 ½-year-olds; the rate apparently increased for animals older than 2 1/ 2. Sex ratio comparisons were inconclusive for fawns but indicated that 1 ½-3 ½-year-old females had a higher mortality rate than males of the same age. The mortality rate of males 4 ½-7 ½ years and older appeared greater than females of the same age group. Food habits were studied from analysis of 14 carcass rumens and 6,113 instances of plant use recorded at 31 pronghorn feeding sites. Rumen contents were characterized by fringed sagewort (*Artemisia frigida*), creeping juniper (*Juniperus horizontalis*), and a variety of forbs. Comparison of rumen samples with feeding site examinations suggested that starvation occurred while animals were restricted to the grassland vegetative type. Among pronghorns in the Glasgow herd fawn production was 39-55 fawns per 100 does as compared to a normal of 90-110. On the Malta winter range where sagebrush was abundant, available, and heavily utilized, losses were minor and fawn production normal. **Key words: antelope, fecundity, nutrition, mortality**

219

Meagher, M. 1976. Winter weather as a population-regulating influence on free-ranging bison in Yellowstone National Park. Pages 29-38 *in* Research in the Parks, Transactions of the National Park Centennial Symposium. National Park Service Symposium Series, Number One. Abstract: Wintering dynamics of three units of the Yellowstone National Park bison population were examined including Pelican, Mary Mountain and Lamar in relation to historic weather conditions. Available records and personal experience were used. Decreases in all population units between 1956 and 1957, which are most striking in the Pelican and Mary Mountain units, coincided with the severe winter of 1955-56. Reported winterkill as an indicator of the amount of late winter mortality suggested the effects winter conditions could exert. Bison in the Hayden Valley segment appear to be less vulnerable to severe winters due to a more varied terrain and vegetation, increasing availability of food and shelter. Some bison also migrate to the Firehole side which experiences less severe weather. **Key words: bison, snow, temperature, movement, nutrition**

220

_____. 1971. Snow as a factor influencing bison distribution and numbers in Pelican Valley, Yellowstone National park. Pages 63-67 *in* A. O. Haugen, ed. Proceedings of the Snow and Ice in Relation to Wildlife and Recreation Symposium. Iowa State University, 11-12 February, Ames, Iowa. Abstract: Bison distribution during any given winter appears directly influenced by snow depths. With average snow depths of 40 to 45 inches in Pelican Valley (settled but not crusted) bison fed extensively on the sedge bottoms of Pelican Creek and its tributaries, and some of the adjacent benches. Groups are more concentrated at this time. As snow depths increase, they scatter more widely and occupy areas of benches and steeper side slopes where wind action may have lessened snow depths. Limited data indicate this shift may occur with 50 to 60 inches of snow. Finally (with perhaps 60 inches and more of snow) some begin to use tree wells—pits around the bases of trees—at the forest

fringes. With these conditions, most that survive have already moved into scattered small thermal areas on Pelican Creek and west of Astringent Creek. Movement for any distance becomes nearly impossible with the deeper snows.

Snow depth appears to be the dominant influence on bison distribution; thus a similar pattern of foraging area use may occur with a more moderate but long winter. With crusting conditions, storms, and extended periods of low temperature there may be a brief use of thermal areas of forest edges which are usually not utilized until snow depths are well above average.

Available weather records suggest that severe winter conditions can be expected to reduce high bison population numbers in Pelican Valley about once each decade. Large decreases in numbers of bison wintering in Pelican coincided with severe winters only when the population was approximately 200 and more in number (1943,1956). At lower population levels (less than 200), decreases were small although severe winter conditions occurred (1965).

Bison are consistently able to endure more severe winter conditions, particularly deep snows, than are the other gregarious species of large mammals in Yellowstone. This is apparently related to their ability to forage in deep snow. **Key words: bison, snow, distribution**

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Mech, L. D. 2004. Is climate change affecting wolf populations in the high Arctic? Climate Change 67:87-93. Abstract: Global climate change may affect wolves in Canada's High Arctic (80° N) acting through three trophic levels (vegetation, herbivores, and wolves). A wolf pack dependent on muskoxen and arctic hares in the Eureka area of Ellesmere Island denned and produced pups most years from at least 1986 through 1997. However, when summer snow covered vegetation in 1997 and 2000 for the first time since records were kept, halving the herbivore nutrition-replenishment period, muskox and hare numbers dropped drastically, and the area stopped supporting denning wolves through 2003. The unusual weather triggering these events was consistent with global-climate-change phenomena. **Key words: snow, predation, muskoxen**

222

_____, D. W. Smith, K. M. Murphy, and D. R. MacNulty. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. Journal of Wildlife Management 65(4):998-1003. Abstract: We studied wolf (*Canis lupus*) predation on elk (*Cervus elaphus*) in Yellowstone National Park from 17 March to 15 April 1997 (severe winter conditions) and from 2 to 31 March 1998 (mild winter conditions) 2-3 years after wolves were reintroduced to the park. Elk composed 91% of 117 kills. Data comparisons for 1997 versus 1998 were: hunting success rate, 26% versus 15%; kill rate, 17.1 kg/wolf/day versus 6.1; percent of kill consumed in first day, 7 versus 86; percent femur marrow fat of adult kills, 27 versus 70; calf:adult ratios of kills, 2:33 versus 17:23; sex ratio of kills, 14M:19F versus 17M:6F; mean age of elk killed, males 6.1 years, females 15.2 versus males, 4.8, females 13.0. Winter severity influenced the wolf-elk relationship more than the naiveté of the elk herd to predation by wolves. **Key words: elk, snow, predation**

223

_____, R. E. McRoberts, R. O. Peterson, and R. E. Page. 1987. Relationship of deer and moose populations to previous winters' snow. Journal of Animal Ecology 56:615--627. Abstract: (1) Linear regression was used to relate snow accumulation during single and consecutive winters with white-tailed deer (*Odocoileus virginianus*) fawn:doe ratios, moose (*Alces alces*) twinning rates and calf:cow ratios, and annual changes in deer and moose populations. Significant relationships were found between snow accumulation during individual winters and these dependent variables during the following year. However, the strongest relationships were between the dependent variables and the sums of the snow accumulations over the previous three winters. The percentage of the variability explained was 36 to 51. (2) Significant relationships were also found between winter vulnerability of moose calves and the sum of the snow accumulations in the current, and up to seven previous, winters, with about 49% of the variability explained. (3) No relationship was found between wolf numbers and the above dependent variables. (4) These relationships imply that winter influences on maternal nutrition can accumulate for several years and that this cumulative effect strongly determines fecundity and/or calf and fawn survivability. Although wolf (*Canis lupus* L.) predation is the main direct mortality agent on fawns and calves, wolf density itself appears to be secondary to winter weather in influencing the deer and moose populations. **Key words: deer, moose, snow, nutrition, mortality**

224

_____, L. D. Frenzel, Jr., and P. D. Karns. 1971. The effect of snow conditions on the vulnerability of white-tailed deer to wolf predation. *In*: L. D. Mech and L. D. Frenzel, eds., Ecological studies of the timber wolf in northeastern Minnesota. USDA Forest Service Research Paper No. NC-52. Snow depth and penetrability (measured with Verme's 1968 apparatus) were measured over 3 winters. The winters 1966-1967 and 1967-1968 were characterized by normal or less than normal snow accumulations. The winter of 1968-1969 was characterized by deep snow, high penetrability until January, then a rapid decrease in penetrability. In January, deer sank in 2.5-3.5 feet. Later, as penetrability decreased, deer still had trouble in moving since support was not adequate for running and the denser snow offered more resistance. Wolves had a much easier time catching deer in February-March 1969. As snow became extremely deep, wolves gained an advantage because of a lesser weight-load-on-track. The high snow density accentuated this difference. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography,* University of BC, Vancouver, BC, Canada, pp. 38-39.) **Key words: white-tailed deer, snow, mortality, predation**

225

Merrill, E. H. 1991. Thermal constraints on use of cover types and activity time of elk. Applied Animal Behavior Science 29:251-267. Abstract: Use of cover types and activity patterns of radio-collared elk (*Cervus elaphus roosevelti*) inhabiting the Mount St. Helens blast zone in the State of Washington, U.S.A., were studied under different climatic conditions. Elk use of forest cover during the midday period was not greater (P<0.12) on clear days than on cloudy days. Estimates of the heat load of a foraging elk

indicated that normal body temperatures could be maintained in the seral plant communities of the blast zone despite high radiative heat gain. An increase in wind speeds in mid to late afternoon suggested an increase in convective heat loss. Additionally, elk became inactive and selected bedding sites with little vegetation. Elk compensated for the decrease in diurnal activity time by increasing nocturnal feeding. Abundant, high quality forage in the Mount St. Helens blast zone most likely facilitated these responses to heat stress. **Key words: elk, wind, temperature, behavior, thermoregulation**

226

Michael, E. D. 1968. Aggressive behavior of white-tailed deer. Southwestern Naturalist 13(4):411-420. Abstract: Aggressive behavior among white-tailed deer (*Odocoileus virginianus*) was observed during a 2-year period on the Rob and Bessie Welder Wildlife Refuge, San Patricio County, Texas. Observations were made from towers and vehicles. Most incidents involving the use of antlers were pushing contests which possibly served to establish hierarchic organization. Only 8 of 94 antler contests were considered to be malicious in which some degree of belligerence occurred. Aggressive behavior in which antlers were used was observed during all months of the year but hostile fights occurred only during the mating season. Hoof fights by bucks occurred when antlers were in the velvet stage or were absent. Hoof fights by does occurred in all months except December and January. Time-of-day, cold fronts, wind speed, cloud cover, and moon phase did not consistently affect aggression by bucks in the same way. Below average temperatures were correlated with an increase in frequency of aggression by bucks. Aggression involving the use of both antlers and hooves followed a uniform pattern with little variation in style. **Key words: white-tailed deer, temperature, wind, clouds, behavior**

227

Miller, F. L. 1970. Distribution of black-tailed deer (*Odocoileus hemionus columbianus*) in relation to environment. Journal of Mammalogy 51(2):248-260. Abstract: During 1964, 1410 hours of observation yielded 6746 sightings of black-tailed deer (*Odocoileus hemionus columbianus*) within the Cedar Creek study enclosure on the Tillamook Burn, Oregon. Deer activity was influenced by age, sex, reproductive phase, extremes or sharp changes in temperature, minimum relative humidity, and precipitation. Deer sought cover by midmorning from mid-May to November when weekly extreme temperatures exceeded 60°F. Their activity was sharply reduced by heavy summer rainfall, but was not influenced by winter rains. Monthly and annual home ranges were related to age and sex, and varied with changes in the reproductive cycle and forage availability. Annual home ranges varied from one-eighth to one-half square mile. **Key words: black-tailed deer, temperature, humidity, precipitation, movement**

228

_____ and A. Gunn. 2003. Catastrophic die-off of Peary caribou on the western Queen Elizabeth Islands, Canadian High Arctic. Arctic 56(4):381-390. Abstract: The Peary caribou (*Rangifer tarandus pearyi*) is an endangered species in Canada, having been in an overall decline since 1961. Sightings of Peary caribou were compared from

two aerial searches, in 1993 and 1998, on Bathurst and its neighboring islands, western Queen Elizabeth Islands in the Canadian High Arctic. The comparison indicated a near total (98%) cataclysmic decline in the number of Peary caribou seen per unit of search efforts. In summer 1993, 2400 caribou were counted during 33.8 hours of low-level helicopter searches. In contrast, in summer 1998, only 43 caribou were seen within the same area during 35.2 h of low-level helicopter searches. The frequency of observation was markedly different: 118.3 caribou/100 min in 1993, but only 2.0 caribou/100 min in 1998. The number of carcasses indicated that the decline resulted from deaths and not from mass emigration. Males died at a disproportionately higher rate than females among all 1+ yr old caribou, and bulls (4+ yr) compared to cows (3+ yr) had died at an even greater rate. Widespread, prolonged, exceptionally severe snow and ice conditions from 1994-95 to 1996-97 caused the die-off. Trends in snowfall are consistent with predictions for global warming in the western Canadian High Arctic. Further climate change may increase the frequency of years with unfavorable snow and ice conditions, which would prevent or at least impede future recovery of Peary caribou populations on the western Queen Elizabeth Islands, particularly to sizes that would support subsistence harvesting. **Key words: caribou, mortality, temperature, nutrition**

229

Miller, G. 1998. A wildlife mortality sample and marrow fat assessment during a record snowfall winter, northwestern Montana. Intermountain Journal of Sciences 4(3/4):102-103. Abstract (only): Carcasses (*n*=114) killed during winter 1996-97 in the lower Clark Fork River drainage of western Montana were examined and assessed for condition by one marrow fat index using visual rating and percent fat (dry/wet weight) rating methods. Species examined were bighorn sheep (*Ovis canadensis*)(*n*=11), elk (*Cervus elaphus*)(*n*=33), mule deer (*Odocoileus hemionus*)(*n*=3), and white-tailed deer (*Odocoileus virginianus*)(*n*=97). Sex, age, femur length, diastema, mortality agent, and parasites were recorded when available. Percent marrow-fat was analyzed on 53 specimens. Most (93%, *n*=29) white-tailed deer that died before 15 February had >20% marrow fat, while 33% (*n*=15) of those that died after 15 February had <20% marrow fat. There was a significant difference between percent marrow fat for those deer that died during the first half of winter and those that died in the last half (*p*=0.003, t-test). A majority (59%, *n*=22) of white-tailed deer carcasses from mid-late winter had an inadequate marrow fat visual rating. A total of 1 (36%) animals were <1 year old (1 elk, 2 bighorn sheep, 38 white-tailed deer) and 14(12%) were estimated at >10 years old (1 elk, 13 white-tailed deer). Females (77%, *n*=85) markedly outnumbered males (*n*=26) in this sample (3 were unknown). Mortality agents were categorized as hunter wasted (1%), predator (7%), road kill (87%), train-kill (4%), and unknown (1%). These data document the seasonal physical stress on a sample of wildlife in northwestern Montana during a record snowfall event and support the contention that weather conditions can have a dramatic impact on wildlife populations. Since this type of data have not been collected in this area prior to 1997, no comparisons can be made regarding physical health during less severe winter conditions. Efforts to collect such data in the future will be made when time and resources allow. **Key words: bighorn, white-tailed deer, elk, mortality, snow**

230

Millspaugh, J. J., K. J. Raedeke, G. C. Brundige, and C. C. Willmott. 1998. Summer bed sites of elk (*Cervus elaphus*) *i*n the Black Hills, South Dakota: considerations for thermal cover management. American Midland Naturalist 139:133-140. Abstract: We characterized 131 summer, diurnal bed sites of 26 elk (11 bulls and 15 cows) in Custer State Park, South Dakota, from 5 June-30 August 1994, 1995 and 1996. Overstory canopy closure, number and basal area of trees, percent litter and bare ground were greater (P<0.05) at bed sites than at random plots. North aspects were selected (P<0.05). Microsite air temperature and percent of grass were lower (P<0.05) at bed sites than at random plots. Hiding cover, wind speed, percent of forbs, shrubs, rocks, and wood, slope percent, average tree dbh, elevation, distance to roads, distance to trails, and distance to water were not different between bed sites and random plots (P>0.05). Trees were present at 128/131 (97.7%) of bed sites (0.01 ha square plot), but occurred on only 41.2% (54/131) of random plots. An average summer, diurnal elk bed site had basal area >12.4 m^2/ha. >100 trees/ha, >54% canopy closure on N aspects. Overstory canopy closure, tree basal area and microsite temperature correctly classified 86.2% of the observations, suggesting thermoregulatory factors influenced CSP elk use of summer, diurnal bed sites. Although elk are successful in some unforested areas despite the lack of suitable thermal cover, our data suggest that elk in the Black Hills prefer relief sites that provide thermal bed sites when available during the summer diurnal period. Management of appropriate thermal cover should be maintained in areas in which it exists. **Key words: elk, thermoregulation, temperature**

231

Milner, J. M., D. A. Elston, and S. D. Albon. 1999. Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. Journal of Animal Ecology 68:1235-1247. Summary: 1. The relative importance of density-dependent and –independent factors on inter-annual variation in over-winter survival was investigated in the fluctuating population of Soay sheep on St Kilda, Scotland, over the period 1985-96. 2. Population density had a negative effect on survival in lambs and adult males while adult female survival showed no evidence of density dependence over the observed range of population densities. 3. Climatic fluctuations associated with the winter North Atlantic oscillation index (NAO) also affected survival, which decreased in winters that were relatively warm, wet and windy. The effect was most pronounced in lambs. 4. Survival was modeled using logistic regression analysis with and without year fitted as a random effect. The former incorporated stochastic year to year variation in survival. Results from the two modeling approaches were similar in terms of the regression coefficients estimated. However, the standard errors of the year-dependent covariates, population size and NAO, were underestimated when the random year effect was ignored, leading to incorrect inferences about the relative significance of terms being made. 5. Using both modeling approaches, density dependence was found to have a greater influence on survival than the effect of NAO in lambs and adult males, whereas in adult females NAO was the more important. 6. Once random between-year effects were taken into account, the individually varying terms such as body weight and fecal egg count were the most significant factors explaining differences in survival. **Key words: mortality, Soay sheep, temperature, precipitation, wind, NAO**

232

Moen, A. N. 1974. Radiant temperatures of hair surfaces. Journal of Range Management 27(5):401-403. Abstract: The radiant temperatures (T_r) of the surfaces of winter pelage of white-tailed deer, mule deer, snowshoe hare, cottontail rabbit, and red fox decrease with a decrease in air temperature T_a) and an increase in wind velocity (U). The relationship between T_r and T_a is linear, but nonlinear for T_r:U. Changes in the lower velocities have a relatively greater effect than changes in the higher velocities. The variation between species results in considerable overlap; the use of thermal scanning techniques for censusing of these different species is doubtful under most field conditions. The feasibility of thermal scanning for censusing purposes is doubtful in all but the simplest of habitats as vegetative cover would further diffuse the thermal image. **Key words: mule deer, white-tailed deer, temperature, wind, census, technique**

233

_____. 1968a. Energy exchange of white-tailed deer, western Minnesota. Ecology 49(4):676-682. Abstract: The energy exchange of white-tailed deer in an open field environment under clear winter skies at night is presented. Environmental radiation flux was measured with field instruments; radiation loss and surface temperature of deer were estimated with a simulator; heat loss by convection, evaporation, and warming ingested food was estimated from methods and data reported in the literature for other species. Metabolic heat production at three dietary levels, environmental radiation flux, and the heat loss at air temperatures from 0° to -40°C and wind velocities from ½ to 12 mph at deer height were integrated to provide a quantitative basis for determining the conditions under which thermal stress commences. Calculations are for fawns and does in a standing position in an open field under clear, nocturnal skies.

The smaller deer reach a negative energy balance at air temperatures approaching 0°C and wind velocities of ½ to 1 mph if they are on a starvation diet. A maintenance to full diet enables them to withstand higher winds and lower temperatures. The larger deer reach a negative energy balance at air temperatures approaching 0°C and wind velocities of 3 mph when on a starvation diet. A full diet, however, enables them to withstand exposure to -40°C temperatures and wind velocities of 8 mph.

The behavior of the animals on the study area indicated that food rather than cover was of major importance in determining the locations where the deer remained during cold weather. Neither wind nor air temperatures to -35°C forced the deer into the protection of the woodlots. The energy balance predicted from the calculations indicated that these weather conditions should not cause a negative energy balance as long as the food supplied an adequate amount of energy and the deer could seek shelter from wind by moving behind a hill, shrub, or herbaceous vegetation in the open fields. **Key words: white-tailed deer, nutrition, wind, temperature**

234

_____. 1968b. Surface temperatures and radiant heat loss from white-tailed deer. Journal of Wildlife Management 32(2):338-344. Abstract: Measurements of surface temperatures and radiant heat loss from the trunks of two penned white-tailed deer (*Odocoileus virginianus*) fawns were made remotely with a portable radiometer during

the winter. Surface temperatures were 6-8 degrees C higher than air temperatures. No difference was observed between the two deer in the surface temperature:air temperature relationships. The difference between air temperature and the surface temperature of the deer increased as air temperature decreased. Measurements of thermal radiation under clear skies at night showed a greater quantity of heat energy emanating from cedar cover than from upland hardwood cover or the clear sky in an open field. The radiant heat from the animal can be integrated with that from the different cover types if the radiation profile of the animal is known. The profile for white-tailed deer has not been determined, but may be estimated. Physiological evidence is cited which indicates the importance of radiant heat when the energy balance of an organism is being considered.

The quantity of heat lost by the animal must be balanced against the heat produced by metabolic processes. Each of the major factors contributing to heat loss, including conduction, convection, radiation, and evaporation, must be considered as well as differences in the amount of heat produced by the animal on different diets and at different levels of activity. Thus the game manager is forced to distinguish between both the quantity and quality of food and cover on a range and their combined energetic effects on the physiological response of the animal. In Minnesota deer in agricultural habitats did not always seek heavier cover during extremely cold winter weather. The deer continued to bed in the open fields and feed on corn, soybeans and dry sweet clover herbage. Data indicate that this was possible, from an energetic standpoint, because the diet supplied an adequate quantity of metabolizable energy, but deer on a range with depleted food quality or quantity may require heavier cover to maintain a positive energy balance. Thermal energy emanating from cover can only reduce heat loss; sufficient food must be available for basal energy requirements and for activity of the animal. **Key words: white-tailed deer, temperature, nutrition**

235

_____ **and F. L. Jacobsen. 1974. Changes in radiant temperature of animal surfaces with wind and radiation. Journal of Wildlife Management 38(2):366-368.** Abstract: There is extreme variability of thermal energy flux from animal surfaces when exposed to ambient conditions. Inanimate objects such as rocks, soil surfaces, vegetation, and other natural objects very likely show variations similar to animals. The problem of differentiating between organisms and objects whose thermal contrasts overlap is considerably more difficult than the mere detection of a source of infrared energy. **Key words: wind, temperature, census, technique**

236

Monson, G. 1960. Effects of climate on desert bighorn sheep numbers. Transactions of the Desert Bighorn Council 4:12-14. Notes: The author notes that the most important variations occur in the amount of rainfall over wind velocity and temperature. The changes in vegetation resulting from variation in precipitation has considerable effect on desert bighorn. A severe drought from 1955 to 1957 led to a reduction in desert bighorn populations. The author found an unusual number of bighorns dead to causes other than predation and disease. He concluded those animals of lowest vitality died during this period due to the impacts of drought on vegetation and moisture availability. The majority of the dead animals were old (over 8 years). He also

noted a drop in the ewe-lamb ratio of summer waterhole counts on Kofa and Cabeza Prieta Game Ranges. **Key words: bighorn, drought, precipitation, mortality, population dynamics**

237

Montana Department of Fish, Wildlife & Parks. 2006. Ecology of white-tailed deer in the Salish Mountains, northwest Montana. Helena, Montana. Summary: Findings specific to winter 1996-1997: 1) A weak yearling age class (1996 cohort) during autumn 1997 among both males and females and low recruitment among the 1997 cohort suggested that this severe winter event substantially affected two year classes; both fawns on the ground from the 1996 cohort and *in-utero* production and/or early neonatal losses from the 1997 cohort; 2) population reconstruction suggested that the lowest rate of overall survival (across all sex and age classes) occurred during 1996-1997, which included the most severe winter on record. However, only yearling recruitment rates were consistently related to winter weather patterns (critical temperature) throughout this study; 3) Non-hunting mortality other than predation was markedly evident only during the severe winter of 1996-1997. Of 22 documented deaths resulting from malnutrition over the period of study, eight occurred during that winter; 4) A combination of harvest regulations directed at antlerless deer on the general deer license (A-tag) and weather probably influenced the dramatic increase in antlerless harvest during autumn 1996 in both hunting districts 101 and 102; 5) Critical temperature, i.e., the cumulative number of days in which minimum daily temperature falls below -12°C (10°F) can be useful to setting quotas for antlerless deer harvests because of relationship between recruitment rates and winter temperatures. **Key words: white-tailed deer, mortality, recruitment, nutrition, temperature**

238

Mooring, M. S., T. A. Fitzpatrick, I. C. Fraser, J. E. Benjamin, D. D. Reisig, and T. T. Nishihira. 2003. Insect-defense behavior by desert bighorn sheep. Southwestern Naturalist 48(4):635-643. Abstract: Biting insects impose costs on hosts, including decreased feeding or resting time as the result of disturbance, blood loss, and disease transmission. Insect-repelling behaviors, such as ear-flicking, head-shaking, stamping, and grouping, have evolved in many ungulate species to minimize these costs. We studied female desert bighorn sheep (*Ovis canadensis mexicana*) at Red Rock Wildlife Area, New Mexico, during the summers of 1999 and 2000. We tested the predictions that: 1) bighorn sheep will increase insect-defense behavior when biting insects are more abundance, and 2) close aggregation of sheep will decrease the per capita insect harassment by means of a dilution effect. Numbers of midges and other biting insects increased in association with rising temperature and decreased with increasing wind speed. Ewes performed between 0 and 78 ear-flicks/min, and >5,000 ear-flicks over the course of a 12-h day. As predicted, the rate of ear-flicking was positively correlated with counts of biting insects, indicating that ear-flicking was a direct response to the irritation of attacking insects. We also found a negative correlation between the number of sheep clustered together within 1 body length and ear-flicking rate, suggesting that insect harassment is diluted when bighorn sheep bunch together. Bighorn sheep generally bedded on upper slopes and rocky outcrops exposed to gusts of wind. These results indicate that ear-flicking, grouping, and microhabitat choice might be important strategies

for reducing the costs of biting insects in desert bighorn sheep. **Key words: wild sheep, insects, temperature, wind**

239

Moran, R. J. 1973. The Rocky Mountain elk in Michigan. Michigan Department of Natural Resources, Research and Development Report 267. Snow cover resulted in a shift in diet from herbs and grasses to one almost completely comprised of browse. **Key words: elk, snow, nutrition**

240

Morris, M. S. and J. E. Schwartz. 1957. Mule deer and elk food habits on the National Bison Range. Journal of Wildlife Management 21(2):189-193. Notes: The authors examined food habits of elk and deer on the National Bison Range in fall 1951 to fall 1952. Conifers made up 74.2 percent of the volume in January deer diets and was exclusively Douglas-fir. They observed that deer may make heavy use of Douglas-fir in November if it is made accessible by wind breakage of trees or by logging. In this case, the low temperatures and deep snow may have caused the deer to yard up on north-facing slopes in young stands of Douglas-fir with resulting heavy use of fir. Snow and low winter temperatures were important factors in conditioning the availability and use of forage in winter. **Key words: deer, snow, wind, temperature, diet**

241

Mörschel, F. M. 1999. Use of climatic data to model the presence of Oestrid flies in caribou herds. Journal of Wildlife Management 63(2):588-593. Abstract: Both caribou and reindeer (*Rangifer tarandus*) are heavily persecuted by warble flies and nasal botflies (*Oestridae*; *Hypoderma tarandi*, *Cephenemyia trompe*), which can have negative effects on these ungulates. Climatic data were collected concurrently with observations of caribou in 1994 and 1995 in the northcentral Alaska Range and used to model presence of oestrid flies. Presence or absence of oestrid flies were indexed by observations of caribou annoyance behavior. Daytime temperature and wind speed were the most important climatic factors affecting oestrid fly presence and were used to build a simple model. The model allows prediction of the probability of oestrid fly presence, based on temperature and wind speed, and may be used to describe the effect of oestrid flies on caribou behavior and population dynamics. **Key words: caribou, insects, temperature, wind, model**

242

Murray, D. L., E. W. Cox, W. B. Ballard, H. A. Whitlaw, M. S. Lenarz, T. W. Custer, T. Barnett, and T. K. Fuller. 2006. Pathogens, nutritional deficiency, and climatic influences on a declining moose population. Wildlife Monographs 166:1-30. Abstract: Several potential proximate causes may be implicated in a recent (post-1984) decline in moose (*Alces alces andersoni*) numbers at their southern range periphery in northwest Minnesota, USA. These causes include deleterious effects of infectious pathogens, some of which are associated with white-tailed deer (*Odocolieus virginianus*), negative effects of climate change, increased food competition with deer or moose, legal or illegal hunting, and increased predation by gray wolves (*Canis lupus*)

and black bears (*Ursus americanus*). Long-standing factors that may have contributed to the moose decline include those typically associated with marginal habitat such as nutritional deficiencies. We examined survival and productivity among radiocollared (*n*=152) adult female and juvenile moose in northwest Minnesota during 1995-2000, and assessed cause of death and pathology through carcass necropsy of radiocollared and non-radiocollared animals.

Aerial moose surveys suggested that hunting was an unlikely source of the numerical decline because the level of harvest was relatively low (i.e., approx. 15%/2 yr) and the population usually grew in years following a hunt. The majority of moose mortalities (up to 87% of radiocollared moose [*n*=76] and up to 65% of non-radiocollared moose [*n*=84%]) were proximally related to pathology associated with parasites and infectious disease. Liver fluke (*Fascioloides magna*) infections apparently constituted the greatest single source of mortality and caused significant pathology in the liver, thoracic and peritoneal cavities, pericardial sac, and lungs. Mortality due to meningeal worm (*Parelaphostrongylus tnuis*) was less prevalent and was manifested through characteristic neurological disease. Several mortalities apparently were associated with unidentified infectious disease, probably acting in close association with malnutrition. Bone-marrow fat was lower for moose dying of natural causes than those dying of anthropogenic factors or accidents, implying that acute malnutrition contributed to moose mortality. Blood profiles from live-captured animals indicated that those dying in the subsequent 18 months were chronically malnourished.

Relative to other populations, average annual survival rates for adult females (0.79)[0.74-0.84; 95% CI]) and yearlings (0.64 [0.48-0.86]) were low, whereas those for calves (0.66[0.53-0.81]) were high. Pregnancy (48%) and twinning (19%) rates were among the lowest reported for moose, with reproductive senescence among females being apparent as early as 8 years. Pregnancy status was related to indices of acute (i.e., bone marrow fat) and chronic (i.e., blood condition indices) malnutrition. Opportunistic carcass recovery indicated that there likely were few prime-aged males (>5 yr old) in the population.

Analysis of protein content in moose browse and fecal samples indicated that food quality was probably adequate to support moose over winter, but the higher fecal protein among animals that died in the subsequent 18 months could be indicative of protein catabolism associated with malnutrition. Trace element analysis from moose livers revealed apparent deficiencies in copper and selenium, but there was limited evidence of direct association between trace element concentrations and moose disease, pathology, or mortality. Time-series analysis of regional moose counts (1961-2000) indicated that annual population growth rate was related negatively to mean summer temperature, with winter and summer temperatures increasing by an average of 6.8 and 2.1C, respectively, during the 40-year period. This change may have increased moose thermoregulatory costs and disrupted their energy balance, and thereby reduced their fitness. Time-series analysis failed to show a relationship between annual population growth rate and moose or deer abundance, indicating that food limitation via resource competition was unlikely. Population viability analyses, using count data (1961-2000) and demographic data collected during this study, suggested that the northwest Minnesota moose population likely would not persist over the next 50 years. More broadly, we conclude that the southern distribution of moose may become restricted in areas where climate and habitat conditions are marginal, especially where deer are

abundant and act as reservoir hosts for parasites. **Key words: moose, nutrition, disease, temperature, thermoregulation**

243

Mysterud, A. and E. Østbye. 2006. Effect of climate and density on individual and population growth of roe deer *Capreolus capreolus* at northern latitudes: the Lier valley, Norway. Wildlife Biology 12(3):321-329. Abstract: The growth of individuals and populations can be affected by both density-dependent and density-independent factors. Severe environmental conditions typically affect young and very old individuals more than prime-aged individuals, so that limiting factors such as climate and density frequently interact with the sex- and age-structure of the population. For roe deer *Capreolus capreolus* explicit analyses of growth rates of individuals and populations at northern latitudes are rare. In this article, we present the first analysis of a 17-year record of body weight data (*N*=286) and harvest statistics (a proxy for population size) from the Lier valley, Norway. We tested whether climate (winter and spring) and population density affected individual body weight in autumn and the growth rate of the population as indicated by harvest statistics. We found that population growth rate in the Lier valley was negatively affected by increasing snow depth during winter. There was also a tendency for body weight to be lower after snowy than after less snowy winters. We found no significant effect of spring temperature or population density, though parameter estimates of both were negative. Our findings provide quantitative data supporting the common knowledge that winter is the critical period for roe deer at northern latitudes, and that population density is unlikely to be a regulating factor in most inland areas of Norway with today's low population densities. **Key words: roe deer, snow, population dynamics**

244

_____, E. Meisingset, R. Langvatn, N. G. Yoccoz, and N. Chr. Stenseth. 2005. Climate-dependent allocation of resources to secondary sexual traits in red deer. Oikos 111:245-252. Abstract: Fitness in highly polygynous male ungulates is related both to body size, weight and antler size. Males must therefore allocate resources both to growth of the body and growth of the antlers, which may lead to tradeoffs whenever resource levels are in limited supply. Several studies have reported how (absolute) growth of antlers and horns are related to environmental conditions, but few have looked for the relative allocation patterns (i.e. relative to body size and weight). We analyzed how the influence of variation in climate (the North Atlantic oscillations, NAO) and population density affected the allocation of resources to antlers, based on data from 2720 red deer stags two years or older harvested during 1965-2002 along the west coast of Norway. Number of antler tines increased up to six years of age, remained stable until 12 years of age, and then decreased significantly (>12 years, *n*=45). The NAO was positively related to number of antler tines in prime aged males (6-12 years; *n*=629), also after controlling for both body size and weight. Our study thus suggests that deer have a higher allocation of resources to antlers relative to body weight during favorable environmental conditions. **Key words: red deer, antler**

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_____, N. G. Yoccoz, N. Chr. Stenseth, and R. Langvatn. 2000. Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. Journal of Animal Ecology 69:959-974. Abstract: 1. Recently, contrasting evidence of density-dependent offspring sex ratio variation in red deer (*Cervus elaphus* L.) has been presented. Kruuk *et al.* (1999) reported that the proportion of male red deer born on the Island of Rum, Scotland, each year declined with increasing population density and with winter rainfall, i.e. as nutritional stress in females increased. In contrast, Post *et al.* (1999a) reported increasing male-biased offspring sex ratios in Hordaland, Norway, with both rising numbers of hinds and increasing values of the North Atlantic Oscillation (NAO), which they regarded an index of severe winters. 2. Compared to Post *et al.* (1999a), we reanalyzed sex ratio variation on a greatly extended data set, including four populations of Norwegian red deer, taking into account a finer population substructure. 3. The proportion of male calves shot each autumn declined markedly as density increased in all four populations. The proportion of male calves shot each autumn increased significantly with an increasing NAO index in one of the four populations, but there was no residual effect of the NAO once the effect of snow depth (at low elevation) was controlled for (decreasingly male biased harvest with increasing snow depth). 4. At the west coast of Norway, the NAO is positively correlated with temperature and precipitation. However, since temperatures in this region often are around 0°C during winter, the relationship between the NAO and snow depth may be difficult to predict. 5. An analysis of variation in snow depth revealed that snow depth was negatively correlated with the NAO at low altitudes (below 400 m), but this relationship was reversed at high altitudes giving a positive correlation between snow depth and the NAO. We therefore suggest that a high NAO index indicates favourable winter conditions for red deer, as red deer winter at low altitude, and since recent studies show that a high index of the NAO is generally positively correlated with body weight in red deer. 6. Female red deer thus reared fewer sons as nutritional stress increased with increasing density and severity of climate in Norway, which is consistent with the birth sex ratios observed on Rum, Scotland. **Key words: red deer, density dependence, NAO, sex ratio**

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Nasimovich, A. A. 1955. The role of the regime of snow cover in the life of ungulates in the USSR. Moskva, Akademy Nauk USSR. Translated from Russian by the Canadian Wildlife Service, Ottawa, Canada. The most ambitious compendium of the effects of snow on ungulates presently available. Chapter I deals with movement of ungulates through snow. Figures 1 and 2 give foot-loadings and chest heights respectively. Animals are separated into “snowshoe-ungulates” (musk deer and reindeer), “stilt-walkers” and “rock-climbers”. Critical depths are given in the species-by-species discussion. The effects of snow crusts on movement are discussed.

Chapter II deals with the effect of snow on ungulate diets. Ungulate species are broken down by the class of forage eaten. The diversity of the winter diet is almost invariably lesser than the summer diet. Ungulates can forage through deeper snow if it is lower density. Reindeer are the most proficient of ungulates in obtaining food from beneath the snow. The winter feeding of many wild and domestic ungulate species is described in some detail.

Chapter III deals with the effect of snow cover on the winter distribution of ungulates. Mountainous areas have the most variability in snow depth and therefore offer the widest choice of habitat selection. Animals often contract their home ranges in winter.

Chapter IV deals at great length with seasonal migrations of ungulates due to snow conditions.

Chapter V discussed intra- and inter-specific relations of ungulates during snowy seasons. In most ungulates, gregariousness is more marked in the winter. Predators gain an advantage over ungulates due to their generally smaller weight-loads-on-track. Table 5 lists weight-loads for predator species. This advantage is to some extent offset by the generally shorter legs of predators. Wolves therefore avoid taiga forests where the snow is deep and powdery; the critical depth is 50 cm.

Chapter VI deals with the effect of snow on ungulate mortality.

Chapter VII treats the effect of snow cover on the configuration of ungulate ranges and ungulate distribution. Hunting can be particularly destructive during winters of deep snow. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography,* University of BC, Vancouver, BC, Canada, pp. 40-41.) **Key words: snow, mortality, distribution, movement, nutrition**

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Natori, Y. and W. P. Porter. 2007. Model of Japanese serow (*Capricornis crispus*) energetics predicts distribution on Honshu, Japan. Ecological Applications 17(5):1441-1459. Abstract: Understanding what determines a species' range is a central objective in ecology and evolutionary biology. It has important applications for predicting species distributions and how they might respond to environmental perturbations. This paper describes a mechanistic approach to predict past and present distribution of the Japanese serow (*Capricornis crispus)* on Honshu, Japan. We applied state-of-the-art microclimate and animal biophysical/behavioral models coupled with climate and vegetation data to estimate the distribution of potential range expansion under protection. We tested the model results against detailed empirical distribution data from the Ministry of the Environment for a five-prefecture area in central Honshu. We also applied the models to time-series land use/cover maps to investigate the historical transitions in habitat suitability during 1947-1999 in the Arai-Keinan region. This is the first time to our knowledge that mechanistic models have successfully predicted the landscape scale distribution of a mammal species in the absence of other animal interactions, such as predators. In this case, animal energetics/behavior-plant interactions seem to be critical. Forest cover appears to be important in summer and winter for suitable serow habitats. The energetics model results indicate that the serow can overheat in some open environments in midday hours in summer. In winter, simulation results suggested that forest cover provides effective refuge to avoid increased metabolic demands of cold temperatures and strong winds. The model simulations suggested that land use/cover changes documented during 1947-1999 resulted in increased suitable serow habitat due to expanding forest cover from agricultural marginalization and ecological succession. The models provide a unique tool for estimating species' range expansion under protection or for selecting suitable reintroduction sites. K**ey words: serow, distribution, model**

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Ndibalema, V. G., S. Mduma, S. Stokke, and R. Røskaft. 2007. Relationship between road dust and ungulate density in Serengeti National Park, Tanzania. African Journal of Ecology. Published on line by Blackwell Scientific. Abstract: We measured the responses of ungulate grazers to roads by recording the density of dust on grasses and compared distance sampling of ungulates in Serengeti National Park (SNP),Tanzania. Data were collected on the east and west side of the Ngorongoro-Seronera main gravel road to test if road traffic and dust were important factors determining distribution patterns amongst grazers. Results indicate that dust increased progressively with traffic speed and volume during dry season. More dust was intercepted on the west than on the east side of the road mainly because of wind effects. Dust deposition (measured as density g grass g^{-1} dust) was higher on short grasses than on long grasses during the dry and late-dry seasons than during the wet season, when paired perpendicular distances up to 300 m were compared. Mean number of observed grazer species indicated that most fed further from the west side of the road than from the east perhaps to minimize higher density of dust commonly spread on foliage up to 200 m away from the road. Despite that most grazers avoided road side grass shoulders, supporting the 'dust aversion hypothesis', the test predictions from the 'road disturbance' and the 'road attraction' hypotheses did not support the responsive behaviors of grazers toward roads. **Key words: wind, movement**

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Nichols, L. 1988. Simple methods of comparing winter snow conditions on alpine and subalpine ranges of Dall's sheep and mountain goats in Alaska. Proceedings of the Biennial Symposium Northern Wild Sheep and Goat Council 6:330-335. Abstract: A simple, inexpensive method was designed whereby one person could rapidly estimate winter snow depth and relative hardness on accessible Dall's sheep (*Ovis dalli*) winter ranges. The method was repeatable and permitted statistical comparisons between areas and years. It also enabled evaluation of snow conditions relative to sheep's foraging ability. Another method utilizing simple aerial photography was used to estimate percent gross snow cover on winter ranges of both Dall's sheep and mountain goats (*Oreamnos americanus*). Again, statistical comparisons could be made between areas and years. Distribution and density of both species were correlated with percent snow cover. **Key words: wild sheep, index, snow**

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Nussey, D. H., T. H. Clutton-Brock, S. D. Albon, J. Pemberton, and L. E. B. Kruuk. 2005. Constraints on plastic responses to climate variation in red deer. Biology Letters 1:457-460. Summary: Influences of climate on life history traits in natural populations are well documented. However, the implications of between-individual variation in phenotypic plasticity underlying observed trait-environment relationships are rarely considered due to the large, long-term datasets required for such analysis. Studies typically present correlations of annual trait means with climate or assume that individual phenotypic responses are constant. Here, we examine this additional level of variation and show that, in a red deer population on the Isle of Rum, Scotland, changes in climate generate changes in phenotype only amongst individuals who have

experienced favorable ecological conditions. Examination of relationships between offspring birth weight and spring temperature within the lifetimes of individual females revealed that the tendency to respond to climate declined as the population density experienced early in life increased. The presence of such systematic variation in individual plasticity is rarely documented in the wild, and has important implications for our understanding of the environmental dependences of traits under varying ecological conditions. **Key words: red deer, phenotype, temperature, population density**

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Oakley, C. and P. Riddle. 1974. The impact of a severe winter and fences on antelope mortality in southcentral Wyoming. Proceedings of the Pronghorn Antelope States Workshop 6:155-173. Abstract: A severe winter storm in southcentral Wyoming forced antelope (*Antilocapra americana*) into a heavily fenced area north of Interstate Highway 80. Fences and the severe winter conditions took a heavy toll on the antelope. A comprehensive study was initiated to evaluate the losses. Utilizing belt transects and population data, several conclusions were made. Overall loss to the antelope herd was an estimated 61.8%; fawns and yearling bucks suffered the highest percent mortality of antelope forced into the fenced complex. Woven wire fences caused the highest mortality. Compared to a relatively fence-free area, mortality per square mile was almost twice as great in the fenced area. Sex and age data indicates that overall, bucks and fawns suffered the highest percent mortality. Yearling buck survival was highest and fawn production was greatest where antelope were not forced through fences. During periods of heavy snow and adverse weather, observations indicate that all types of fences were detrimental to antelope. **Key words: antelope, snow, fences, mortality, temperature**

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Oehler, M. W., R. T. Bowyer, and V. C. Bleich. 2003. Home ranges of female mountain sheep, *Ovis canadensis nelsoni*: effects of precipitation in a desert ecosystem. Mammalia 67(3):385-401. Abstract: We compared sizes of home ranges and other ecological variables for female mountain sheep (*Ovis canadensis nelsoni*) inhabiting climatologically distinct areas in the Mojave Desert, California, USA. We also examined the relationship between size of home range and body size and age of mountain sheep. The pattern of precipitation was uni-modal in the more xeric Panamint Range, and bimodal at Old Dad Peak. Density of female sheep was about four times greater at Old Dad Peak than in the Panamint Range; Old Dad Peak also had more shrubs and perennial grasses than the Panamint Range. Home ranges and core areas were nearly twice as large in the Panamint Range than at Old Dad Peak, and females at Old Dad Peak were consistently nearer water. We detected no relationships between size of body or age and size of home-ranges for female mountain sheep. Females at Old Dad Peak foraged predominantly on perennial grasses and forbs, whereas those in the more xeric Panamint Range consumed mostly shrubs, perennial forbs, and succulents. In general, quality of forage was higher at Old Dad Peak than in the Panamint Range. Fecal nitrogen did not differ between areas in spring, but was higher in the Panamint Range during summer and autumn. We conclude that mountain sheep from the Panamint Range had larger home ranges because of lower availability and quality of forage, ostensibly a consequence of that precipitation regime. Use of cacti by mountain

sheep in the Panamint Range likely enhanced the ability of females to increase the area in which they foraged in that depauperate and xeric environment. We hypothesize that pattern and amount of precipitation and subsequent productivity of plants, affect the distribution of mountain sheep, and ultimately probabilities of persistence for populations of these mountain ungulates. **Key words: bighorn, precipitation, distribution**

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Ogutu, J. O., H.-P. Piepho, H. T. Dublin, N. Bhola, and R. S. Reid. 2008. Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. Journal of Animal Ecology, *Online Early,* Blackwell-Synergy, 14-April 2008: 1-16.
Summary: 1. Rainfall is the prime climatic factor underpinning the dynamics of African savanna ungulates, but no study has analyzed its influence on the abundance of these ungulates at monthly to multi-annual time scales. 2. We report relationships between rainfall and changes in age- and sex-structured abundances of seven ungulate species monitored monthly for 15 years using vehicle ground counts in the Maasai Mara National Reserve, Kenya. 3. Abundance showed strong and curvilinear relationships with current and cumulative rainfall, with older topi, *Damaliscus korrigum* (Ogilby); warthog, *Phacochoerus aethiopicus* (Pallas); waterbuck, *Kobus ellipsyprimnus* (Ogilby); and impala, *Aepyceros melampus* (Lichtenstein) responding to longer lags than younger animals, portraying carryover effects of prior habitat conditions. 4. The abundances of newborn calves were best correlated with monthly rainfall averaged over the preceding 5-6 months for topi, waterbuck, warthog, and 2 months for the migratory zebra *Equus burchelli* (Grant), but with seasonal rainfall averaged over 2-5 years for giraffe, *Giraffa camelopardalis* (L.); impala; and kongoni, *Alcelaphus busephalus* (Pallas). The cumulative late wet-season rainfall was the best predictor of abundance for quarter- to full-grown animals for most species. Monthly rainfall exert both negative and positive effects on the abundances of zebra, impala and waterbuck. Ignoring age, both sexes responded similarly to rainfall. 5. Births were strongly seasonal only for warthog and topi, but peaked between August and December for most species. Hence abundance was strongly seasonal for young topi and warthog and the migratory zebra. Pronounced seasonality in births for warthog and topi obliterated otherwise strong relationships between abundance and rainfall when both month and rainfall were included in the same model. Aggregated density produced relationships with rainfall similar to those for fully grown animals, emphasizing the necessity of demographic monitoring to reliably reveal rainfall influences on ungulate abundance in the Mara. 6. Strong relationships between abundance and rainfall suggest that rainfall underpins the dynamics of African savanna ungulates, and that changes in rainfall due to global warming may markedly alter the abundance and diversity of these mammals. Ungulates respond to rainfall fluctuations through movements, reproduction or survival, and the responses appear independent of breeding phenology and synchrony, dietary guild, or degree of water dependence. Newborns and adults have contrasting responses to rainfall. Males and females respond similarly to rainfall when age is ignored. **Key words: precipitation, ENSO, temperature, population dynamics**

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_____ and N. Owen-Smith. 2005. Oscillations in large mammal populations: are they related to predation or rainfall? African Journal of Ecology 43:332-339.

Abstract: Cyclic population dynamics is relatively common among populations of small mammals in high latitudes but is not yet established among African savanna ungulates. However, oscillations may be expected in large mammal populations subject to quasi-periodic oscillations in regional rainfall. We evaluated evidence for environmentally entrained oscillations in a large-mammal predator-prey system in Kruger National Park (KNP), South Africa, where rainfall exhibits quasi-periodic oscillations. The evaluation is based on analysis of comparative changes in the abundance of twelve ungulate species throughout South Africa's KNP using population counts over the period 1965-1996. We present evidence suggesting that (i) twelve ungulate populations display cyclic variability with half-periods ranging between 10 and 18 years, (ii) this variability was associated with lagged rainfall between 3 and 10 years back in the past for different ungulate species, and (iii) the ungulate species respond in contrasting ways to rainfall, with some reaching highest abundance during periods of low rainfall and others under conditions of high rainfall. These findings are not consistent with the response pattern we would expect if the population oscillations were driven directly by the rainfall influence on food availability. Instead they seem to be an outcome of predator-prey interactions, which are entrained by the effect of rainfall on habitat conditions affecting the relative susceptibility of the different ungulate species to predation. **Key words: precipitation, predation**

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_____ **and N. Owen-Smith. 2003. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. Ecology Letters 6:412-419.** Abstract: Climatic variation associated with the North Atlantic Oscillation (NAO) and El Niño-Southern Oscillation (ENSO) has a widespread influence on the population dynamics of many organisms worldwide. While previous analyses have related the dynamics of northern ungulates to the NAO, there has been no comparable assessment for the species rich assemblages of tropical and subtropical Africa. Census records for 11 ungulate species in South Africa's Kruger National Park over 1977-96 reveal severe population declines by seven species, which were inadequately explained by indices of ENSO or its effects on annual rainfall totals. An additional influence was an extreme reduction in dry season rainfall, concurrent with and perhaps related to a regional temperature rise, possibly a signal of global warming. Boundary fencing now restricts range shifts by such large mammals in response to climatic variation. Our models project near extirpation of three ungulate species from the park's fauna should these climatic conditions recur. **Key words: precipitation, temperature, ENSO, fences, migration, mortality**

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Olson, K. A., T. K. Fuller, G. B. Schaller, B. Lhagvasuren, and D. Odonkhuu. 2005. Reproduction, neonatal weights, and first-year survival of Mongolian gazelles (*Procapra gutturosa*). Journal of Zoology, London 265(3):227-233. Abstract: Mongolian gazelles *Procapra gutturosa* were observed, hand-captured and radio-monitored in the eastern steppe of Mongolia during 1998-2003 to understand better their reproduction and survival. During early June, 92% (range = 87-96%) of adult (≥2 years old) females observed (mean *n* = 735/year) were pregnant, and nearly all gave birth during a 10-day interval (24 June- 3 July) each year. Mean mass of neonate (1-2 days old) calves (mean *n* = 47/year) was greater for males than for females, and masses were

directly correlated with mean monthly temperatures the previous winter (December-April). Survival during the first 10 days of life for 111 radio-marked neonate calves monitored during 2000-03 (*n* = 9-55/year) was 0.83 and did not seem to vary with birth weight. Also, deaths owing to hypothermia, abandonment, or unknown causes (interval cause-specific mortality rate = 0.16) outnumbered deaths owing to predation (0.02) during this interval. Survival rates were similar during the rest of the year (0.86 for 355 days) when most mortalities were owing to predation (interval mortality rate = 0.12 *vs* 0.01). Annual survival of calves was 0.71 (95% CI = 0.61-0.82). Gazelle births are highly synchronous, probably to take most advantage of the short summer growing season, and perhaps to avoid deleterious spring weather and to minimize predation. High fecundity and relatively high calf survival, especially during the first weeks of life, support the notion that gazelle populations can recover fairly quickly from demographic catastrophes. **Key words: gazelle, temperature, mortality, fecundity**

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Ontario Ministry of Natural Resources. n.d. The snow network for Ontario wildlife: the why, when, what and how to winter severity assessment in Ontario. Abstract: A snow network has been operating in Ontario since 1952, providing information about provincial winter severity. Efforts have been made to ensure adequate provincial representation (mainly by research staff), but the operation of individual courses has depended largely on the perceived values to local staff, and funding.

Although the Snow Network for Ontario Wildlife (SNOW) was designed primarily for use in deer management, the data generated can be used by wildlife managers to monitor the effects of winter conditions on many wildlife species. It will help the Ontario Ministry of Natural Resources (OMNR) meet the requirements of the Terms and Conditions of the Timber EA by helping to understand population trends of indicator forest species. The information aids in management decisions regarding game harvest limits and regulations, and reintroduction programs for such economically important species as deer, moose, wild turkey and elk. The financial investment and income generated by hunting deer, moose and other game can be protected by effective population management which includes SNOW data.

SNOW has recently been automated through the province-wide OMNR computer network and the SNOW data management program, allowing access to historical data and providing greater uniformity in measurement.

In recent years, lack of funding and manpower has led to a deterioration of the network, and district decisions to close many snow courses. Immediate needs to create and maintain a standard provincial network include travel or contract funds for measurements at distant courses and funds to replace or repair course equipment.

The purpose of this plan is to design a minimum network of snow courses which will avoid redundancy and adequately cover the variation of winter severity across the province, providing information to wildlife and fire and flood managers, biologists, and the general public. With suitable funding in place and adherence to guidelines for SNOW winter severity measurement, the OMNR can provide effective and efficient monitoring of winter conditions across Ontario. **Key words: index, snow, monitoring**

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Owen, J. G. 1990. Patterns of mammalian species richness in relation to temperature, productivity, and variance in elevation. Journal of Mammalogy 71(1):1-13. Abstract: In Texas, the relationship between environmental factors and species richness of all mammals, bats, rodents, and carnivores was investigated by multiple-regression methods. Variance in elevation was a strong, positive predictor of species richness for all mammals, bats (*Chiroptera*), and rodents (*Rodentia*). It was a significant but weak predictor for carnivores (*Carnivora*). Productivity had significant, negative regression coefficients for all mammals, bats, and rodents. Productivity was positive, significant, and relatively stronger for carnivores. Species richness of all mammals, rodents, and carnivores may follow a hump-shaped curve along a gradient of increasing environmental productivity. Mean-annual temperature range was significant with a negative sign for carnivores and with a positive sign for rodents. Mean intermonthly variability of precipitation had a positive and significant relationship to carnivores, but significant, negative coefficients for bats and rodents. Variation in all mammals and carnivore species richness, and in all mammals and bat richness, was significant, with positive signs, for maximum and minimum temperatures, of record, respectively. All mammals, bat, and rodent richness varied significantly, with negative signs, with the coefficient of variation of mean January temperature. Overall, the climatic-variability indices exhibited only weak control over density of mammalian species. With the exception of productivity their influence on current ecological hypotheses of species richness was complex. Statistical support, contradiction, and statistical lack of significance depended upon the particular combination of environmental factors and taxa under consideration. Results suggest that current ecological hypotheses of species richness often function in directions not concordant with predictions and are not satisfactory as general explanations of biotic richness for these vertebrate groups. **Key words: productivity, temperature**

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Owen-Smith, N. 1990. Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. Journal of Animal Ecology 59(3):893-913. Summary: (1) The study was conducted from 1974 to 1984 in two areas of the Kruger National Park differing in mean rainfall. Age-class specific survival rates were estimated by individual registration of the kudus present in each female-young social unit, using natural markings. (2) The kudu populations in both study areas increased in 1974-78 then declined in 1978-83. Because of high annual variability in juvenile recruitment, no stable age distribution was attained. (3) The survival rates of juveniles (including prenatal losses), yearlings and old females (> 6 years of age) were significantly correlated with the preceding annual rainfall total. Rainfall over the late wet season exerted the strongest influence. A negative relation was evident between survival and preceding biomass density of kudus, which was statistically significant for juveniles. For prime females only a weak relation between survival rates and both variables combined was shown in the lower rainfall study area. (4) Survival rates were significantly correlated with resource supply relative to population demand, as indexed by the rainfall/biomass ratio, except in the case of prime females. Data points for both study areas fitted closely similar regression lines, indicating that the higher kudu density in one area counterbalanced the higher mean rainfall there. (5) Juvenile survival post-

conception functioned as the key factor causing population fluctuations as well as being density-dependent. Prime females in the age range 2-5 years conferred a degree of population resilience to drought, due to their insensitivity to resource limitations. (6) Rainfall is presumed to act through its effects on the food supply, in particular of high quality components such as forbs. However, the effects of wet season rainfall on juvenile survival appeared to be partially density-independent. Predation was probably responsible for a background mortality level of 5-10% per annum even among prime-aged animals. Although all mortality was probably mediated by predation, except during a severe drought year, fluctuations in mortality were evidently dependent on nutritional well-being as influenced by rainfall relative to kudu density. (7) Where the resource supply fluctuates widely between years, as is the case where it is controlled by rainfall, density-dependent effects may become evident only after controlling for such fluctuations. This is especially true for herbivores dependent on food quality as well as quantity. The influence of rainfall variability on population dynamics can be opposite in sign for browsing and grazing ungulates. **Key words: precipitation, drought, kudu, population dynamics**

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_____, D. R. Mason, and J. O. Ogutu. 2005. Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. Journal of Animal Ecology 74:774-788. Summary: (1) Through reconciling census totals with population structure, annual survival rates were estimated for the juvenile, yearling and adult stages of 10 ungulate species over 14 years or longer in South Africa's Kruger National Park. During this period four species maintained high abundance levels, while six species declined progressively in abundance. (2) Multiple regression models fitted to these estimates indicated that juvenile survival was sensitive to annual variability in rainfall for most of these species, especially in the dry season component, but with no density feedback apparent. Rainfall components affected adult survival in several of the declining species, while negative density dependence in adult survival was evident for three of the four species that maintained high abundance. A negative effect of past prey availability, indexing putative changes in predator abundance, on adult survival was more strongly supported statistically among the declining species than the lagged effect of prior rainfall, potentially affecting herbaceous vegetation cover and composition. (3) The high sensitivity of juvenile survival to environmental variability among these ungulate species was consistent with the general pattern identified for large mammalian herbivores, although the absence of any survival response counteracting the density declines was surprising. The susceptibility of adult survival to environmental influences for the declining species appeared unusual and probably reflected an interaction between nutritional shortfalls and a numerical increase in lions, preying largely upon the adult segment of these species. The ungulate species that persisted at high abundance seemed resistant to effects of rainfall on food resources and evidently drove the changes in predator abundance. The sharp density effect on adult survival among these species could indicate prey switching by lions following changes in their relative availability. (4) Findings extend past generalizations about the demographic processes underlying the population dynamics of large mammalian herbivores and reveal how the survival rates of particular population segments respond differently to environmental influences. Demographic patterns help reveal the interplay of changing resource supplies, predation

pressure and population abundance on population changes. **Key words: precipitation, density, predation**

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Ozoga, J. J. 1968. Variations in microclimate in a conifer swamp deeryard in northern Michigan. Journal of Wildlife Management 32(3):574-585. Abstract: Wide differences in winter microclimate were found in 1965 and 1966 among six habitat types within a single conifer swamp used by white-tailed deer (*Odocoileus virginianus*) as a winter yarding area in Upper Michigan. No compartment of cover provided both optimal shelter and adequate food. A densely stocked even-aged stand of mature swamp conifers offered deer the best protection from cold weather and the least hazardous snow conditions. This site exhibited the narrowest thermal ranges, warmest average temperatures during the coldest weather, highest and most stable relative humidity, least amount of wind flow, minimal snow depths, and best snow support conditions. The other habitat types consisted of pole-size and sapling conifers, mixed hardwood-conifers, northern hardwoods, and upland opening. Since deer normally seek the best shelter available from adverse climatic factors, management of conifer swamp deeryards should strive to maintain blocks of even-aged mature timber as prime winter cover, interspersed in an ideal pattern near younger stands providing abundant food. **Key words: white-tailed deer, wind, snow, temperature, habitat use**

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_____. and L. W. Gysel.1972. Response of white-tailed deer to winter weather. Journal of Wildlife Management 36(3):892-896. Abstract: Mechanical traffic counters were used to monitor daily activity of white-tailed deer (*Odocoileus virginianus*) in a conifer swamp deeryard in northern Lower Michigan during the winter of 1963-64. Findings indicate that use of protective (dense) cover by deer increased during periods of low temperature and high calculated air chill, despite the lack of deep snow. We assume that differences in recorded activity actually represent shelter-seeking movements of deer into the conifer swamp in response to increasing severity of weather. Based on 748 traffic counts, the most consistent peak of deer activity occurred from mid- to late afternoon, 60 percent of the movement being recorded between sunrise and sunset. **Key words: white-tailed deer, wind, behavior**

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Parker, K. L. 1988. Effects of heat, cold, and rain on coastal black-tailed deer. Canadian Journal of Zoology 66:2475-2483. Abstract: Thermoregulatory responses of black-tailed deer (*Odocoileus hemionus columbianus*) were recorded in a metabolic chamber at dry air temperatures between -20 and 32°C. For animals in summer pelage, respiratory rates, body core temperatures, and skin temperatures increased curvilinearly with increasing air temperature; thermally critical air temperatures occurred above 27°C and below 10°C. In winter, body temperatures were lower in adults than in fawns, skin temperatures were highly variable, and respiratory rates increased at lower air temperatures than in summer; metabolic expenditures associated with thermoregulation increased at temperatures less than -10°C. Animals were also subjected to simulated rain (4.5 mm/h) over a 5-h period at temperatures above freezing. During summer trials

in the rain, body and skin temperatures generally declined after 5 h. No increased metabolic stress associated with rain was observed for black-tailed deer in summer at air temperatures greater than 12°C; at 10°C, energy expenditures after 5 h of rainfall were greater than during heat or cold stress. For animals in winter pelage, changes in body temperature, skin temperature, and hair depth showed no consistent trends with duration of rainfall; only fawns increased metabolism at temperatures just above freezing (2-3°C) in the rain. Data from this study suggest that rainfall may pose major energetic constraints for black-tailed deer in summer pelage. Managerial provisions for thermal cover should place highest emphasis on summer habitats. **Key words: black-tailed deer, precipitation, thermoregulation**

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_____ **and M. P. Gillingham. 1990. Estimates of critical thermal environments for mule deer. Journal of Range Management 43(1):73-81.** Abstract: Mule deer (*Odocoileus hemionus hemionus*) can be thermally stressed under a wide range of ambient conditions. We developed a model that provides examples of the combinations of wind, solar radiation, and air temperature that may result in thermally critical environments for standing, full-fed adult mule deer during winter in snow-covered and snow-free, open habitats, and in meadows in summer. Critical thermal combinations of environmental variables are shown as 3-dimensional surfaces and tables. Animal size, age, pelage characteristics, and ground cover (height and albedo) further affect the energy costs for thermoregulation by mule deer. The need for habitat managers to consider the provision of thermal cover to reduce heat or cold stress in mule deer depends on the combinations of environmental variables in a particular habitat and geographic location. Implications, limitations, and management considerations of our estimates are discussed. **Key words: mule deer, thermoregulation, wind, solar radiation, temperature**

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_____**, C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48(2):474-488.** Abstract: Energy expenditures for several activities were measured using indirect calorimetry with five mule deer (*Odocoileus hemionus*) and eight elk (*Cervus elaphus nelsoni*). The average energetic increment of standing over lying was 25%. Net energy costs (kcal/kg/km) of horizontal locomotion without snow decreased as a function of increasing body weight. The average cost per kilogram for each vertical meter climbed on a 14.3° incline was 5.9 kcal. Efficiency of upslope locomotion averaged 40-45% for the two species; downslope efficiency decreased with increasing body size. Energy expenditures for locomotion in snow increased curvilinearly as a function of snow depth and density. To further understand the energetics of locomotion in snow, foot loading and leg length were measured. Management implications, based on the costs of locomotion for mule deer and elk when disturbed by winter recreationists and when traversing the slash deposition of logging operations, are discussed. Logging affects energy requirements of elk and deer by influencing snow depth through removal of canopy interception of falling snow. Management should consider restricting human access to ungulate winter use areas if maximum survival of ungulate herds is a primary concern. **Key words: mule deer, elk, movement, bioenergetics, snow**

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Parmesan, C., T. L. Root, and M. R. Willig. 2000. Impacts of extreme weather and climate on terrestrial biota. Bulletin of the American Meteorological Society 81(3): 443-450. Abstract: Climate is a driver of biotic systems. It affects individual fitness, population dynamics, distribution and abundance of species, and ecosystem structure and function. Regional variation in climatic regimes creates selective pressures for the evolution of locally adapted physiologies, morphological adaptations (e.g., color patterns, surface textures, body shapes and sizes), and behavioral adaptations (e.g., foraging strategies and breeding systems). In the absence of humans, broad-scale, long-term consequences of climatic warming on wild organisms are generally predictable. Evidence from Pleistocene glaciations indicates that most species responded ecologically by shifting their ranges poleward and upward in elevation, rather than evolutionary through local adaptation (e.g., morphological changes). But these broad patterns tell us little about the relative importance of gradual climatic trends as compared to extreme weather events in shaping these processes. Here, evidence is brought forward that extreme weather events can be implicated as mechanistic drivers of broad ecological responses to climatic trends. They are, therefore, essential to include in predictive biological models, such as doubled CO_2 scenarios. **Key words: model**

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Patterson, B. R. and V. A. Power. 2004. Contributions of forage competition, harvest, and climate fluctuation to changes in population growth of northern white-tailed deer. Oecologia 130(1):62-71. Abstract: Recently there has been considerable interest in determining the relative roles of endogenous (density-dependent) and exogenous (density-independent) factors in driving the population dynamics of free-ranging ungulates. We used time-series analysis to estimate the relative contributions of density-dependent forage competition, climatic fluctuation, and harvesting on the population dynamics of white-tailed deer (*Odocoileus virginianus*) in Nova Scotia, Canada, from 1983 to 2000. A model incorporating the population density 2 years previous, an interaction term for the harvest of females and population density 2 years previous, and the total snowfall during the previous 2 winters explained 80% of the variation in inter-annual population growth rate. Natality of adult females was negatively related to deer density during the present winter, whereas that of yearlings may have been correlated with the snowfall of three winters previous. Natality of fawns was related to deer density and total snowfall during the previous winter. Coyotes (*Canis latrans)* prey extensively on deer fawns in northeastern North America and the annual harvest of snowshoe hares *(Lepus americanus),* the major alternate prey of coyotes, explained 48% of the inter-annual variation in fawn recruitment. The proportions of fawn, yearling, and adult deer suffering from severe malnutrition during late winter were all correlated with deer density during the present winter. We conclude that the limiting effects of winter weather on over-winter survival of deer may be cumulative over two consecutive winters. During the late 1980's, density dependence and winter severity acted in concert to effect substantial declines in deer population growth both by effecting winter losses directly and by exacerbating predation by coyotes. During this period liberal harvesting did not relieve density-dependent forage competition and probably accelerated the decline. **Key words: white-tailed deer, snow, density dependence, predation**

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_____ and F. Messier. 2000. Factors influencing killing rates of white-tailed deer by coyotes in eastern Canada. Journal of Wildlife Management 64(3):721-732.
Abstract: Predation affects the dynamics of many ungulate species. Until recently, little attention has been given to understanding the underlying processes and relationships in predator-prey systems. We examined factors affecting killing rates of white-tailed deer (*Odocoileus virginianus*) by coyotes (*Canus latrans*) in Nova Scotia, Canada. Snowshoe hare (*Lepus americanus*) and deer abundance, distribution and relative vulnerability of deer, and coyote group size all significantly influenced killing rates of deer by coyotes in winter. Groups of coyotes initiated proportionately more chases than single coyotes but chase success differed little among groups of 1-4 coyotes. Snow depth had a positive influence on success of pursuits. More kills were observed in areas of low deer density relative to areas with high deer densities. The mean distance of deer kills to recent clearcuts was significantly shorter than expected in an area where deer yarded during winter, but not in an area where deer did not aggregate during winter. Predator-prey ratios may not be a reliable indicator of predation rates of deer by coyotes because factors such as relative abundance and vulnerability of alternate prey, winter severity, and coyote social behavior also influenced killing rates. **Key words: white-tailed deer, predation, snow**

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Peek, J. M., R. J. Mackie, and G. I. Dusek. 1992. Over-winter survival strategies of North American cervidae. Alces Supplement 1:156-161. Abstract: Adaptations relating to over-winter survival in North American *Cervidae* (*Alces alces, Cervus elaphus, Odocoileus hemiounus, O. virginianus, Rangifer tarandus*) are reviewed. All species adapt by varying physiological and behavioral mechanisms consistent with energy conservation. Adaptations of major importance are decreases in metabolism and activity that become pronounced as environmental conditions restrict access to quality forage. Shifts and adjustments to lower quality forage are accompanied by decline in forage intake and use of habitat which ameliorate weather conditions. Secondary adaptations include social behavior and resource partitioning based on sex and social rank. **Key words: elk, mule deer, caribou, white-tailed deer, habitat use, wind, behavior, thermoregulation**

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Pépin, D., J. Joachim and E. Ferrié. 1997. Variability of spring habitat selection by isards (*Rupicapra pyrenaica*). Canadian Journal of Zoology 75:1955-1965.
Abstract: We studied the influence of snow cover and habitat heterogeneity on altitudinal distribution, grouping patterns, and habitat selection in the isard or Pyrenean chamois (*Rupicapra pyrenaica*) in a protected area from the beginning of May to mid-June 1992. Data were recorded from a single vantage point that allowed visual observations to be made over a wide range of elevations. Variations occurred in the spatial extension of groups, with no sightings above 1900 m when snow was abundant at high altitude and only a few sightings below 1700 m when small patches remained at high altitude. During a late heavy snowfall, however, most sightings were made at the middle altitudinal

range, where adjoining habitats of steep terrain provided areas of reduced snow depth. The frequency of observations of solitary animals increased slightly and was higher in closed than in open habitats. Both a significant habitat effect and a significant interaction between habitat and time period of observations were found for groups of the average size, ≥2 individuals. Montane pastures at low altitude were first selected. Then, when snow melted, this habitat was vacated from 1800- to 2000-m subalpine pastures. Regardless of the time period, the areas dominated by rhododendrons and rocks or scree were systematically avoided. We suggest that in order to gain a better understanding of habitat selection by large ungulates, especially in mountainous areas, short-term variations in environmental heterogeneity be considered. **Key words: chamois, snow**

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_____, R. Faivre, and P. Menaut. 1996. Factors affecting the relationship between body mass and age in the izard. Journal of Mammalogy 77(2):351-358. Abstract: We investigated the influence of gender, capture period, and between-year variation on the relationship between body mass and age in the izard (*Rupricapra pyrenaica*) using data obtained on 201 individuals captured in a Pyrenean reserve, France. Body mass was measured in spring or autumn 1984-1993. Absence of sexual dimorphism in body mass probably resulted from the high density of this protected population. Strong quadratic relationships between age and body mass were observed for spring and autumn (r^2 + 0.79 and 0.76, respectively). Izards exhibited lower body mass in spring than in the previous autumn irrespective of age class. No significant between-year variation occurred in body mass in autumn. There were marked differences between years in spring that may be related to previous climatic conditions in winter, particularly daily temperature in December and total snowfall from November to April. **Key words: temperature, snow, chamois**

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Peterson, R. O. and D. L. Allen. 1974. Snow conditions as a parameter in moose-wolf relationships. Naturaliste Canadien 101:481-492. A study of wolf-moose relationships in relation to snow conditions on Isle Royale. Snow hardness was measured with a compaction gauge comprising a 1.98 cm^2 area statically loaded with up to 650 g cm^{-2}. Overstory was found to decrease snow depth by 29% in one plot and 15% in another. Penetration was 30% greater under the canopy. A total of 220 fresh tracks of 17 moose were measured and an average foot-loading of 230 g cm^{-2} was determined. This is less than the 420-1000 g cm^{-2} reported in other studies. Wolves were found to have foot loadings of 100 g cm^{-2}. Significantly more moose were killed in areas of > 51 cm snow depth. During deep snow periods, both moose and wolves used shorelines for travel and encountered each other more frequently. More calves were killed when snow depths were > 76 cm. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography,* University of BC, Vancouver, BC, Canada, p. 43.) **Key words: moose, snow, mortality, predation**

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Petocz, R. G. 1973. The effect of snow cover on the social behavior of bighorn rams and mountain goats. Canadian Journal of Zoology 51:987-993. Abstract:The social behavior of bighorn rams (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*) were studied quantitatively under different snow regimes in two winters. It was found that snow cover has little noticeable effect on the intensity of social behavior for mountain sheep during the rutting season. Thick snow cover reduces the total number of social behavior patterns per ram during the postrut; among mountain goats the number of social behavior patterns per individual remains consistently high. The thickness of the snow cover effects circumstantial changes in the function of specific behavior patterns among rams. Under extreme snow conditions, rams begin to exhibit rarely seen aggressive behavior. During deep snow, both species show an increase in overt aggressive behavior and a reduction in dominance displays. Under conditions of low snow and favorable weather rams increasingly engage in clashing, dominance displays, and appeasement behavior and reduce aggressive butting. **Key words: wild sheep, mountain goats, snow, behavior**

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Pettorelli, N., R. B. Weladji, Ø. Holand, A. Mysterud, H. Breie, and N. Chr. Stenseth. 2005. The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass. Biology Letters 1:24-26. Abstract: The relative importance of winter harshness and early summer foraging conditions are of prime interest when assessing the effect of global warming on arctic and mountainous ecosystems. We explored how climate and vegetation onset (satellite-derived normalized difference vegetation index data) determined individual performance in three reindeer populations (data on 27,814 calves sampled over 11 years). Snow conditions, spring temperatures and topography were the main determinants of the onset of the vegetation. An earlier onset positively affected the body mass of calves born the following autumn, while there was no significant direct negative impact of the previous winter. This study underlines the major impact of winter and spring climatic conditions, determining the spring and summer food availability, and the subsequent growth of calves among alpine herbivores. **Key words: caribou, index, NAO, temperature, snow, topography**

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_____, A. Mysterud, N. G. Yoccoz, R. Langvatn, and N. Chr. Stenseth. 2005. Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. Proceedings of the Royal Society B 272:2357-2364. Abstract: Understanding how climate influences ecosystems represents a challenge in ecology and natural resource management. Although we know that climate affects plant phenology and herbivore performances at any single site, no study was directly coupled the topography-climate interaction (i.e. the climatological downscaling process) with large-scale vegetation dynamics and animal performances. Here we show how climatic variability (measured by the North Atlantic oscillation “NAO”) interacts with local topography in determining the vegetative greenness (as measured by the normalized difference vegetation index ‘NDVI’) and the body masses and seasonal movements of

red deer (*Cervus elaphus*) in Norway. Warm springs induced an earlier onset of vegetation, resulting in earlier migration and higher body masses. Increasing values of the winter-NAO corresponded to less snow at low altitude (warmer, more precipitation results in more rain), but more snow at high altitude (colder, more precipitation corresponds to more snow) relative to winters with low winter-NAO. An increasing NAO thus results in a spatially more variable phenology, offering migrating deer an extended period with access to high-quality forage leading to increased body mass. Our results emphasize the importance of incorporating spring as well as the interaction between winter climate and topography when aiming at understanding how plant and animal respond to climate change. **Key words: red deer, movement, NAO**

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Picton, H. D. 1994. Horn growth in Montana bighorn rams. Proceedings of the Biennial Symposium, Northern Wild Sheep and Goat Council 9:99-103. Abstract: Annual growth increments of 59 bighorn rams (*Ovis canadensis canadensis*) from 18 Montana hunting districts were analyzed to test several current hypotheses concerning horn growth. Fluctuating asymmetry measurements were used to test the hypothesis that the small horn syndrome of certain herds resulted from population bottlenecking and a resulting loss of genetic variability. Mineral analyses were used to test the hypothesis that horn size differences can be explained by mineral composition differences which serve as indicators of major soil fertility differences among ranges. Neither of these hypotheses was supported by the analytical results. The general pattern of growth was highest in the middle years of life. The sheep from ranges producing large horns showed greater annual growth from the 2nd or 3rd year through life than did the sheep from ranges yielding smaller horn sizes. Patterns of horn growth in transplanted sheep populations resembled the parent population but had considerably larger annual growth increments. Fluctuating asymmetry values were smallest in the sheep from areas producing small horns. This suggests that loss of genetic variability was not a major influence on these sheep. Asymmetry values in transplanted populations resembled the parent population and sibling populations more than unrelated populations. When climatic effects were evaluated, the annual variation in precipitation accounted for about 30% of the annual variation in horn growth after the effects of age were accounted for. **Key words: wild sheep, horn, precipitation**

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_____. 1984. Climate and the prediction of reproduction of three ungulate species. Journal of Applied Ecology 21:869-879. Summary: The Lamb climate index was used to compare temperature and precipitation data to long term population data concerning wapiti (*Cervus elaphus*), mule deer (*Odocoileus heminonus*) and bighorn sheep (*Ovis canadensis*). Significant correlations between survival of young and climate were found for all three species. The intensity of the climate effect was dependent upon the size of the population in relation to carrying capacity (*K*). The wintering wapiti population was negatively correlated with the survival of bighorn sheep lambs. The temperature and precipitation over an 18-month period was important to the recruitment of young in both cervid species. Bighorn sheep integrated climate over a 12-month period, with precipitation being of prime importance to the survival of lambs. These differences, in the response to climate, are probably related to the evolutionary history and modern

geographical distribution of the species. Wapiti calf/cow ratios were correlated with the 2-year moving hunting harvest totals at population levels below carrying capacity (*K*). Winter snow pack was relevant to the survival of bighorn sheep lambs, and to a lesser degree, to mule deer fawns. The results of several predictive methods were compared. Two climate based and one hunting harvest based predictions gave superior results. These point forecasts of the young to adult ratios had mean absolute errors ranging from 7·1-14·9% of the long term mean and had the highest percentage of correct trend forecasts. **Key words: model, elk, mule deer, wild sheep, snow, temperature, precipitation**

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_____. 1979. A climate index and mule deer fawn survival in Montana. International Journal of Biometeorology 23(2):115-122. Abstract: A sign of deviation type of index was used to convert standard temperature and precipitation data into a readily used form for the study of deer population dynamics. Statistically significant correlations between the climate index and mule deer fawn survival were demonstrated for four different mule deer populations in Montana. These correlations led to reasonable biological hypotheses delineating the linkage between climate and fawn survival in each of the four areas. The correlations support the frequent observations in the wildlife literature concerning the importance of summer and winter range. They also suggest that human activities may interact with climate in a manner which affects deer fawn survival. In general, in these areas, fawn survival was favored by relatively warm-moist summer, warm-dry winter and cool-dry hunting season weather. The apparent affect of spring weather was variable. Fawn survival in two areas was enhanced by cool-dry summer weather. This reversed response could be the result of human use of the areas, including livestock grazing. It is concluded that this index of climatic fluctuations can be a versatile and useful tool in assessing the impact of climate upon deer populations. In general, weather can be described as *a strong biasing factor even when direct effects cannot be consistently demonstrated.* **Key words: mule deer, index, temperature, precipitation**

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_____ and R. R. Knight. 1971. A numerical index of winter conditions of use in big game management. Pages 29-38 *in* Arnold O. Haugen, ed., Proceedings of the snow and ice in relation to wildlife and recreation symposium, February 11-12. Abstract: A method for computing a low cost numerical index for comparison of winter conditions was worked out using standard U.S. Weather Bureau data. The use and the biological validity of the index was demonstrated by assessing winter elk counts. Annual elk counts compared with population estimates and index computations indicated that maximum elk observability coincided with winters having index ratings of 1500 or above. This correlation reflects the concentration of elk on winter ranges, the use of cover during the morning hours and improved visibility provided by a uniform contrasting background. Attempts to correlate the winter index with utilization of vegetation were complicated by changes in animal populations during the study period. **Key words: index, elk, census**

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Pioz, M., A. Loison, D. Gauthier, P. Gibert, J-M Jullien, M. Artois, and E. Gilot-Fromont. 2008. Diseases and reproductive success in a wild mammal: example in the alpine chamois. Oecologia 155:691-704. Abstract: Density-dependent and climatic factors affect reproduction and dynamics of wild ungulates. Parasites can also decrease reproductive success through either a direct abortive effect or a negative impact on horn growth and body condition However, few studies have investigated the effect of parasitism on fecundity of ungulates in natural condition. We studied three bacterial infections caused by *Salmonella enterica* serovar Abortusovis, *Chlamydophila abortus* and *Coxiella burnetii*. These bacteria are leading causes of reproductive failure in sheep, goat and cattle, which raises the question of their influence on population dynamics of wild ungulates. A long-term study of demography and epidemiology of an alpine chamois (*Rupicapra rupicapra,* L.) population (Les Bauges Reserve, France) and a generalized linear modeling approach were used to analyze the reproductive success of chamois according to population density, weather conditions and the prevalence of antibodies against the three bacteria in females. This approach enabled us to identify the confounding effect of weather and parasitism on fecundity in a natural population. After accounting for density, the prevalence of antibodies against the three bacteria explained 36% of the annual variation in reproductive success, and weather conditions explained an additional 31%. This study was, to our knowledge, the first to compare the decrease in fecundity due to bacterial infections and weather conditions in a population of wild mountain ungulates. The prevalence of *Salmonella* was negatively correlated with NAO (r = -0.48, P = 0.05); prevalence was higher in spring-summer when the previous winter was cold and snowy. Second, the prevalence of *Coxiella* was positively correlated with snowfall during March-April (r = 0.55, P = 0.02). NAO and snowfall during March-April contributed to explaining variation in reproductive success. Reproductive success was positively correlated with NAO and negatively with snowfall in spring. Overall, climatic conditions may facilitate both disease transmission and expression. **Key words: disease, density, chamois, fecundity, temperature, snow**

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Poole, K. G. and G. Mowat. 2005. Winter habitat relationships of deer and elk in the temperate interior mountains of British Columbia. Wildlife Society Bulletin 33(4):1288-1302. Abstract: Recent work has examined ultimate factors limiting deer (*Odocoileus* spp.) and elk (*Cervus elaphus*) populations during winter, such as temperature and forage, but there has been inadequate examination of the influence of snow, especially in concert with foraging decisions. We examined deer and elk habitat selection on winter range in the temperate mountains of southeastern British Columbia. The life histories of radiocollared mule deer (*O. hemionus*) and elk included seasonal elevational migrations (1,000-1,400 m) and long-distance movements (up to 50-63 km, respectively). Late-winter, deep-snow habitat is limited in wet, mountainous environs and may explain the relatively low densities of ungulates present. Snow-track transects conducted during late winter suggested that deer (mule deer and white-tailed deer [*O. virginianus*] combined) avoided areas with >40 cm of snow and elk areas with >50 cm. Late-winter snow depth was positively related to elevation and negatively related to slope and solar radiation (hours/day), all of which can be obtained from existing databases and used to map relative late-winter snow depth. The snow-depth model can

be used to map potential winter range regardless of current vegetation cover. During late winter deer selected older forests and stands with greater amounts of Douglas-fir (*Pseudotsuga menziesii*) in the overstory in forested sites. Older stands probably were selected because they had lower snow depths, while mature Douglas-fir trees offered more litterfall forage than other tree species. In contrast, elk selection among forested stands was weak, which suggested that forested stands were not preferred portions of their late-winter habitat. Track data during late winter confirmed that both deer and elk also used areas with low canopy cover, likely to acquire browse. We demonstrated that it is possible to map potential winter range using topographic variables as surrogates for relative snow depth, and we present a model applicable to portions of the temperate interior mountains. We suggest it is important to consider both forage production and snow interception in habitat management because winter energy budgets are a balance between nutrient intake and cost of locomotion. **Key words: elk, deer, movement, temperature, snow, technique**

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Portier, C., M. Festa-Bianchet, J. M. Gaillard, J. T. Jorgenson, and N. G. Yoccoz. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). Journal of Zoology London 245:271-278. Abstract: Density-dependence in juvenile survival may be difficult to detect if survival is also affected by density-independent factors. We investigated the relationships among weather parameters, population density, and lamb survival of bighorn sheep with long-term data from a marked population where we manipulated population density. We distinguished neonatal survival and winter survival. Density interacted with weather variables to affect neonatal survival; spring and winter temperatures had a positive effect on neonatal survival only when population density was high. Neonatal survival was positively affected by spring precipitation independently of population density. Winter survival was positively correlated with temperature and precipitation during the previous spring, negatively correlated with density, and independent of winter temperature or snowfall. The effect of weather on lamb winter survival did not vary with density. Bighorn lambs are well adapted to harsh winter weather, but spring weather influenced survival of lambs at birth and during the subsequent winter, possibly through its effects on forage availability. Our study clearly demonstrates density-dependence in lamb survival. Some of the effects of weather on lamb survival are density-independent, others are mediated by an interaction with population density. **Key words: wild sheep, population dynamics**

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Post, E., M. C. Forchhammer, N. Chr. Stenseth, and R. Langvatn. 1999. Extrinsic modification of vertebrate sex ratios by climatic variation. American Naturalist 154(2):194-204. Abstract: Evidence for the influences of climate on early development, maternal condition, and offspring viability in terrestrial vertebrates suggests that climatic change has the potential to induce variation in offspring sex ratios in such organisms. Using long-term data at individual and population levels, we investigated the influence of global climatic variation, as a result of the North Atlantic Oscillation (NAO), on offspring sex ratios of red deer in Norway. The state of the NAO during the fetal development of hinds influenced the mass of their sons, but not daughters, and increasingly warmer and snowy winters led to increasingly male-biased offspring sex ratios, independently of

changes in the mean age of hinds. Moreover, hinds that were themselves born following warm, snowy winters were smaller as adults, produced significantly lighter sons, and tended to produce more sons than hinds born following cold, dry winters. In light of the fact that these observations defy explanation according to previous hypotheses of adaptive modification of offspring sex ratios, we present the extrinsic modification hypothesis, which suggests that sex ratios may evolve in variable environments through natural selection independently of maternal strategies of sex allocation. **Key words: red deer, NAO, sex ratio, snow, temperature**

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_____, R. Langvatn, M. C. Forchhammer, and N. Chr. Stenseth. 1999. Environmental variation shapes sexual dimorphism in red deer. Proceedings of the National Academy of Sciences of the United States of America 96(8):4467-4471. Abstract: Sexual dimorphism results from dichotomous selection on male and female strategies of growth in relation to reproduction. In polygynous mammals, these strategies reflect sexual selection on males for access to females and competitive selection on females for access to food. Consequently, in such species, males display rapid early growth to large adult size, whereas females invest in condition and early sexual maturity at the expense of size. Hence, the magnitude of adult size dimorphism should be susceptible to divergence of the sexes in response to environmental factors differentially influencing their growth to reproduction. We show that divergent growth of male and female red deer after 32 years of winter warming and 15 years of contemporaneously earlier plant phenology support this prediction. In response to warmer climate during their early development, males grew more rapidly and increased in size, while female size declined. Conversely, females, but not males, responded to earlier plant phenology with increased investment in condition and earlier reproduction. Accordingly, adult size dimorphism increased in relation to warmer climate, whereas it declined in relation to forage quality. Thus, the evolutionary trajectories of growth related to reproduction in the sexes (1) originate from sexual and competitive selection, (2) produce sexual size dimorphism, and (3) are molded by environmental variation. **Key words: red deer, temperature, forage quality**

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_____ and N. Chr. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80(4):1322-1339. Abstract: Models of climate change predict that global temperatures and precipitation will increase within the next century, with the most pronounced changes occurring in northern latitudes and during winter. A large-scale atmospheric phenomenon, the North Atlantic Oscillation (NAO), is a strong determinant of both interannual variation and decadal trends in temperatures and precipitation during winter in northern latitudes, and its recent persistence in one extreme phase may be a substantial component of increases in global temperatures. Hence, we investigated the influences of large-scale climatic variability on plant phenology and ungulate population ecology by incorporating the NAO in statistical analyses of previously published data on: (1) the timing of flowering by plants in Norway, and (2) phenotypic and demographic variation in populations of northern ungulates. We analyzed 137 time series on plant phenology for 13 species of plants in Norway spanning up to 50 yr (44±0.5 yr, mean ± 1 SE) and 39 time series on phenotypic and

demographic traits of 7 species of northern ungulates from 16 populations in North America and northern Europe spanning up to 30 yr (18±2.0 yr).

Plant phenology was significantly related to the NAO in 97 time series (71% of the total), in which dynamics of the NAO explained, on average, between 9% and 28% of the interannual variation in flowering dates. Following increasingly warm, wet winters, most plant species (9 of 13 species) bloomed earlier by an average of 13.0±0.8 d to 26.4±1.8 d, (mean±1 SE), one-third (4 of 11 species) bloomed longer by 13.4±1.1 d to 18.8±1.7 d, and there was an increase in spatial variability in timing of flowering across landscapes by five of six species. Woody plants displayed less sensitivity to climatic variability than did herbaceous species, and early-blooming plants were more strongly influenced by the NAO than were late-blooming plants.

Ungulate phenotypic and demographic variables were significantly related to the NAO in 28 time series (72% of the total). Large-scale climatic variability influenced growth, development, fecundity, and demographic trends of all seven species of ungulates studied, and in some populations, the NAO acted together with density dependence. Individuals within mainland populations responded to winter warming with reduced body size and increased fecundity, whereas winter warming in maritime regions led to increased body size by reduced fecundity. Across sex and age classes, between 43% and 70% of the observed range in body mass among years was attributable to the dynamics of the NAO, and within cohorts of female red deer and reindeer, 47-70% of the observed range in fecundity was related to the NAO during the winter preceding cohort birth years. All but two populations of northern ungulates declined following increasingly warmer winters, and the NAO operated, in most instances, in concert with direct density dependence to limit populations. In comparison to the original analyses of these ungulate time series, in 10 of 19 series the NAO explained an equal or greater percentage of variation than that explained by local weather. These observations indicate that large-scale climatic variability has a detectable influence on the ecology of plants land animals in a variety of terrestrial ecosystems, and that the responses of plants to winter warming may, surprisingly, be more subtle than the responses of large herbivores. **Key words: NAO, temperature, population dynamics, fecundity**

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_____ **and N. Chr. Stenseth. 1998. Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. Journal of Animal Ecology 67:537-543.**
Abstract: 1. Mech *et al.* (1987) documented cumulative, negative effects of previous winters' snow on rates of population increase in moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*), but noted no effect of predation by wolves (*Canis lupus*). Those results were contested by Messier (1991), who analyzed smoothed versions of the original abundance data and reported no effect of snow accumulation on population dynamics of either species, but strong effects of wolf predation and food competition. 2. McRoberts, Mech & Peterson (1995) contended that the conclusions reached by Messier (1991) were an artifact of the use of smoothed data. In a subsequent reanalysis of the smoothed data, Messier (1995) argued that the lack of an effect of snow after one year precluded the potential for a cumulative effect beyond one year. 3. We re-analyzed original and smoothed data on dynamics of moose and white-tailed deer densities using the same methods as Mech *et al*. (1987) and Messier (1991), but we used a measure of global climatic fluctuation, the North Atlantic Oscillation (NAO) index. The NAO is the

atmospheric process determining most interannual variation in snowfall and winter temperatures in northern latitudes, and its phases drive decadal trends in wintertime precipitation. 4. We observed that rates of increase of moose and white-tailed deer in both the original and smoothed data were influenced by global climatic fluctuation at 2- and 3-year lags, as well as by delayed density-dependent feedback and wolf predation. **Key words: moose, NAO, white-tailed deer**

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_____, N. Chr. Stenseth, R. Langvatn, and J-M Fromentin. 1997. Global climate change and phenotypic variation among red deer cohorts. *in* Proceedings of the Royal Society of London B 264:1317-1324. Abstract: The variability of two fitness-related phenotypic traits (body weight and a mandibular skeletal ratio) was analysed among cohorts and age-classes of red deer in Norway. Phenotypic variation among cohorts was pronounced for calves, yearlings and reproductively mature adults. Fluctuations in cohort-specific mean body weights and skeletal ratios of adults correlated with global climatic variation in winter conditions influenced by the North Atlantic Oscillation while cohorts were *in utero*. Red deer born following warm winters were smaller than those born after cold winters, and this inter-cohort variability persisted into adulthood. Phenotypic variation among cohorts of red deer influenced by climate change may pose consequences for fitness of cohorts since body size and condition contribute to reproductive success and survival in male and female red deer. In particular, the recent trend of increasingly warm winters in northern Europe and Scandinavia may lead to reduced body size and fecundity of red deer, and perhaps other ungulates, in those areas. **Key words: red deer, temperature, morphology, fecundity**

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Pruitt, Jr., W. O. 1981. Application of the Värriö Snow Index to overwintering North American barren-ground caribou (*Rangifer tarandus arcticus*). Canadian Field-Naturalist 95:363-365. Summary: Pruitt applied his snow index to North American caribou. He concluded that caribou can detect differences in thickness, hardness, and density of api (snow cover of the forest floor). He also discovered that there are thresholds of these snow cover characteristics that caribou do not transgress. Most of the animal's winter movements could be explained by analysis of api morphology according to the author. Pruitt observed that a hard layer in the upper half of the api seems more important in deterring feeding than a layer of equal hardness in the lower half. He notes that surface hardness is probably more important than any other single characteristic because caribou test it directly. **Key words: caribou, snow, movement, nutrition, ice**

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_____. 1979. A numerical "snow index" for reindeer (*Rangifer tarandus*) winter ecology (Mammalia, Cervidae). Annales Zoologici Fennici 16(4):27280. Abstract: Previous work has shown that some ecological characteristics of tundra upsik that are important to small mammals can be expressed by a mathematical model or a "Snow Index". Using results of my own and other investigators' earlier work, plus results of some 460 snow profiles taken in winter 1976-77 in the vicinity of Värriö Subarctic

Research Station in Northeastern Finland, in relation to the semi-domesticated reindeer of Salla North association, I have derived a mathematical model which relates reindeer activity to features of the snow cover. The Värriö Snow Index (VSI) incorporates the hardness of the hardest layer in the upper half of the snow cover, the hardness and thickness of the basal layer, the vertical hardness of the snow cover surface, the thickness of the topmost layer, the harness and thickness of the hardest layer in the snow cover and the total thickness of the snow cover. The VSI agrees well with the winter feeding activities of reindeer near the Research Station and also correlates with the puzzling late-winter movement of the reindeer through the altitudinal tree line into the alpine zone of Värriötunturi. A field check of the VSI in the central part of northern Finland, in the northern part of Kyrö association, where herding is practiced, revealed further agreement, and indicated additional, classifiable snow-reindeer relationships. **Key words: reindeer, snow, index**

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_____. 1960. Animals in snow. Scientific American 202(1):60-68. Discussed the metamorphosis of snow into categories described by aboriginal snow terms. A glossary of these terms is included. The critical hardness and depth of tundra snow to caribou are 60 g cm^{-2} and 2 ft respectively. Caribou movements are constrained by "fences" of snow with unfavorable characteristics. Moose have adapted to snow by developing long legs. The alternative to the moose's "stilt" adaptation is the hare's snowshoe adaptation. Small animals, with unfavorable surface-volume ratios must live beneath the snow surface. Pleistocene megafaunal extinctions may have been due to increased snowfalls. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography,* University of BC, Vancouver, BC, Canada, pp. 45-46.) **Key words: snow, mortality**

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_____. 1959. Snow as a factor in the winter ecology of the barren ground caribou. Arctic 12:159-179. Summary: (1) During the winter 1957-1958 114 snow observation stations were established in parts of northern Saskatchewan and the southern Northwest Territories. Approximately 8,850 miles were flown at low altitudes over the region. During these flights the positions of bands and wintering individuals of Barren Ground caribou (*Rangifer arcticus*) were plotted on topographic maps. (2) Numerous ground observations were made of caribou behavior in relation to snow conditions. (3) The areas of heavy caribou concentration were characterized by snow cover that was quite soft, light, and thin (hardness range of 6.5 to 60 gm./sq/cm. for forest stations and 50 to 700 gm./sq.cm. for lake stations; density range of 0.13 to 0.20 for forest stations and 0.13 to 0.32 for lake stations; thickness range of 19 to 59 cm.). (4) The areas of no caribou were characterized by snow cover that was sometimes soft but also could be very hard, dense, and thick (hardness range of 35 to 7,000 gm./sq.cm. for forest stations and 150 to 9,000 gm./sq. cm. for lake stations; density range of 0.16 to 0.92 for lake stations; thickness range of 19 to 82 cm.). (5) Caribou appear to have a threshold of sensitivity to the hardness, density and thickness of the snow cover. The threshold of hardness sensitivity appears to be approximately 50 gm./sq. cm. for forest snow and 500 gm./sq.cm. for lake snow. The density threshold appears to be approximately 0.19 or 0.20 for forest snow and 0.25 or 0.30 for lake snow. The thickness threshold appears to

be approximately 60 cm. When these thresholds are exceeded caribou react by moving until they encounter snow of smaller hardness, density or thickness. (6) Caribou will dig feeding craters only twice in a given unit of snow after which it becomes so hard that they seek undisturbed snow for feeding. (7) Some of the relationships of snow to the evolution, behaviour, species survival and management of caribou are discussed. (8) Various aspects of necessary future research and improvements in techniques are enumerated and discussed. **Key words: caribou, snow, behavior**

292

Putkonen, J. and G. Roe. 2003. Rain-on-snow events impact soil temperatures and affect ungulate survival. Geophysical Research Letters 30(4):37/1-37/4. Summary: Rain-on-snow events can substantially increase sub-snowpack soil temperatures. Such events can result in widespread die-offs of ungulates due to soil surface icing. We demonstrate that wintertime rain-on-snow events, although infrequent, are capable of exerting a considerable influence on mean wintertime soil temperatures. **Key words: elk, caribou, muskoxen, mortality, precipitation, snow, temperature, ice**

293

Rachlow, J. L. and R. T. Bowyer. 1991. Interannual variation in timing and synchrony of parturition in Dall's sheep. Journal of Mammalogy 72(3):487-492. Abstract: Timing and synchrony of parturition in Dall's sheep (*Ovis dalli*) were studied in Igloo Mountain, Denali National Park and Preserve, Alaska, from April through July 1988 and 1989. Mean ±SD dates of birth were 18 May (±5.1 days) in 1988 and 27 May (±8.8 days) in 1989. Ninety percent of births occurred in a 27-day period in 1988 and in a 36-day period in 1989; interannual variation in timing and synchrony of parturition was pronounced. Mortality of young in this predator-rich environment, however, did not differ between years, suggesting climatic variability may contribute more than predation in constraining timing and synchrony of parturition in Dall's sheep. Weather may affect movements of mountain sheep to traditional rutting grounds, thereby influencing timing of conception. Lastly, weather and plant phenology at time of parturition affect lamb survivorship. **Key words: wild sheep, parturition, snow, movement**

294

Raganella-Pelliccioni, E., L. Boitani, and S. Toso. 2006. Ecological correlates of roe deer fawn survival in a sub-Mediterranean population. Canadian Journal of Zoology 84:1505-1512. Abstract: We investigated the effect of body mass, spring and summer total rainfall, birth period, and local population density on the survival of 130 roe deer (*Capreolus capreolus (*L., 1758)) fawns captured over seven fawning seasons (1997-2003) and radio-monitored daily. We modeled survival using the program MARK, incorporating biological questions into different models, following *a priori* hypotheses. The best model was selected using Akaike's information criterion. The population was surveyed by counts and estimates were obtained using mark-resight methods. Weekly survival of roe deer fawns exhibits a pseudo-threshold time trend. Probability of survival is low (0.33±0.0046) in summer, increases (0.79±0.0021) in fall, and approaches the highest value typical of adult survival (0.90±0.00091) and 0.96±0.00021 by the end of March and May, respectively) during early spring following birth. The final model predicts

that survival of roe deer fawns is positively affected by total precipitation in spring and body mass under a pseudo-threshold time variation pattern. In contrast with other studies, we did not detect any effect of population density on survival of fawns. This study contributes to the scarce knowledge about the performance of roe deer populations in Mediterranean ecosystems, providing evidence that climate variables and individual characteristics shape the vital rates of roe deer populations. **Key words: roe deer, precipitation, parturition**

295

Ratcliff, H. M. and L. Sumner. 1945. National park wildlife ranges. North American Wildlife Conference 10:246-250. Notes: “In the early days of unrestricted grazing, the bighorn of what is now Lava Beds National Monument were exterminated during a winter of unusually heavy snowfall, because practically all of the forage had been previously removed by domestic stock. Sagehens dwindled to the vanishing point because of this competition with domestic stock, although a few individuals have survived in the region. In recent years more conservative grazing practices in the Monument have considerably reduced the yearly damage caused by sheep. Although the native bighorn will never again be seen on their ancestral trails, which show clearly on the pumice slopes of buttes that dot the area, it is possible that the sage hens may some day be restored, when grazing pressure on the range is further reduced. **Key words: snow, wild sheep, mortality, nutrition**

296

Rautenstraugh, K. R. and P. R. Krausman. 1989. Influence of water availability and rainfall on movements of desert mule deer. Journal of Mammalogy 70(1):197-201. The authors describe movements of desert mule deer in an area of southwest Arizona having limited rainfall and few permanent water sources. Their objectives were to determine the influence of availability of water and rainfall patterns on movements of desert mule deer; to test the hypothesis that animals in xeric regions have larger home ranges than conspecifics in more mesic regions; and test the hypothesis that desert mule deer inhabiting an area with geographically unpredictable summer rainfall move to that part of their home range that receives the greatest rainfall and has the most nutritious and succulent forage, as do some ungulates and other large mammals living in deserts. Comparison of the distance from random locations to water and locations of deer to water, indicated that deer were influenced by permanent water sources only during the summer dry season. Deer were further ($P<0.05$) from permanent water than random locations (mean = 7.7 km) during the summer wet, winter, and spring seasons, but closer to permanent water during the summer dry season (mean = 9.1, 9.9, 8.5 and 4.6 km, respectively). Migratory deer moved to their summer-dry-season home ranges from 30 days before to 10 days after that season started in both years. We conclude that migratory deer moved to their summer-dry-season home ranges to find drinking water. Migrations from summer-dry-season ranges corresponded with the start of the summer rains. All deer returned from their summer-dry-season ranges to the same areas they occupied the previous winter and spring instead of migrating to areas receiving the greatest summer rainfall. The synchronized movements away from summer-dry-season ranges suggest that deer had a strong motive to leave those ranges. **Key words: mule deer, precipitation, habitat use, movement**

297

Reimers, E., N. Holmengen, and A. Mysterud. 2005. Life-history variation of wild reindeer (*Rangifer tarandus*) in the highly productive North Ottadalen region, Norway. Journal of Zoology, London 265:53-62. Abstract: Variation in life history is a central key to understanding population dynamics, and density dependence and climate are important factors in shaping life-history variation in ungulates. Early growth is often sensitive to adverse conditions and this may in turn affect juvenile survival and age at first reproduction. We report variation in body weight of 5079 reindeer *Rangifer tarandus* from the North Ottadalen, a very productive reindeer area in Norway, sampled over 14 years in the period 1967-1989. The North Ottadalen reindeer herd was established in 1964 from a winter herd of some 500 semi-domestic reindeer, and allowed to grow to a peak of over 3300 reindeer in 1974, after which increased harvest decreased the population size. The proportion of lactating yearling females varied between 0% and 50%. Lactating females had lower autumn body weights than non-lactating females. A decline in body weight with age, i.e. senescence, was evident in both males and females from around 7 to 9 years of age. Body weights of all age and sex groups as well as the proportion of yearling females lactating decreased over time, and more so in younger than older males, although the population size declined markedly after the population peak in 1974. We found no effect of the North Atlantic Oscillation or local weather on body weight. The possible causes of the marked decline in performance with time in the North Ottadalen reindeer herd are discussed, and it is suggested that this may be related to the transition from being managed as semi-domestic to wild (i.e. hunted). **Key words: reindeer, NAO**

298

Reneker, L. A. and R. J. Hudson. 1990. Behavioral and thermoregulatory responses of moose to high ambient temperatures and insect harassment in aspen-dominated forests. Alces 26:66-72. Abstract: Heart rate and insect annoyance were studied in hand-reared adult moose (*Alces alces*) cows released into a 65-ha enclosure in April, May, July, and October. Radiant heat load exerted the greatest influence on heart rates of bedded moose in all months. Wind and insects had lesser, but significant, effect during April and May, respectively. Respiratory rate was related to ambient temperature showing a dramatic increase above 14°C. **Key words: moose, temperature, wind, insects, thermoregulation, behavior**

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_____, _____, M. K. Christophersen, and C. Arelis. 1978. Effect of posture, feeding, low temperature, and wind on energy expenditures of moose calves. Proceedings North American Moose Conference and Workshop 14:126-140. Abstract: Energy expenditures of two moose calves (*Alces alces*) were studied during late fall and early winter. Interactions of level of feeding, temperature, and posture were examined using a closed-circuit indirect calorimeter. Interactions of temperature and wind were determined in a wind tunnel using the Douglas-bag technique. Increments in energy expenditure due to feeding were approximately 20% over resting metabolism. The energy cost of maintaining a standing posture was in the order of 35%. As temperature dropped from

-20°C to -30°C, metabolic rate increased 36% while standing, but only 2% while lying. Wind speeds up to 8 m sec^{-1} increased energy expenditures consistently only at temperatures below -20°C. **Key words: moose, temperature, wind, bioenergetics**

300

Retzer, V., K. Nadrowski, and G. Miehe. 2006. Variation of precipitation and its effect on phytomass production and consumption by livestock and large wild herbivores along an altitudinal gradient during a drought, South Gobi, Mongolia. Journal of Arid Environments 66:135-150. Abstract: The mountain ranges of southern Mongolia provide traditional pasture for livestock but also habitat for wildlife species, some of which are internationally rare and endangered (e.g. argali). Data from a 1-year field study show that the mountains receive higher precipitation than the surrounding semi-deserts and that this results in a gradient of phytomass production and therefore also in a gradient of forage availability.

Animal observations indicate that livestock generally outnumber large wild herbivores by a factor of 60 on the pediments and by a factor of 6 in the mountains. Moreover, during the drought in the summer of 2001 livestock intruded into argali and ibex habitat. This resulted in additional pressure on those animals through increased forage competition with livestock and increased frequency in anthropogenic disturbance.

Thus, while the use of the mountain steppes as reserves during drought is an opportunistic strategy employed by nomadic herders in a highly variable semi-arid ecosystem, it may interfere with nature conservation efforts for argali. Protection is especially needed during times of stress, while during years of abundant forage the potential for conflict is much lower. Furthermore, the problem may increase under changing climatic conditions. **Key words: precipitation, wild sheep, drought, forage quality**

301

Riley, S. J. and A. R. Dood. 1984. Summer movements, home range, habitat use and behavior of mule deer fawns. Journal of Wildlife Management 48(4):1302-1310. Notes: Below normal precipitation resulted in poor forb production during spring-summer 1977 and 1980. During those summers, does made an early switch from forbs to browse. In turn, fawns made greater and earlier use of timbered cover types that provided the densest hiding cover. **Key words: mule deer, precipitation, habitat use**

302

Robinette, W.L., O. Julander, J. S. Gashwiler, and J. G. Smith. 1952. Winter mortality of mule deer in Utah in relation to range condition. Journal of Wildlife Management 16(3):289-299. Summary: Deer mortality and range condition studies were made following the winter of 1948-49 which, according to the U.S. Weather Bureau, was the severest Utah winter on record. Detailed studies on three Utah winter mule deer ranges revealed that winter deer loss varied inversely with the forage supply. Herd losses of 9, 26, and 42 percent were determined for the three areas on which forage inventories showed that there has been respectively 57, 13, and 9 pounds of green forage present at the start of winter for each deer day of use on the areas. As

winter closed in much of this forage was made unavailable resulting in serious food shortages on two overbrowsed ranges.

Observations of winter deer losses on the study areas and in other herds during moderate and severe winters indicate that on properly stocked ranges the loss is only slightly greater during severe winters than it is during moderate winters. On the other hand, the loss on depleted ranges in severe winters may exceed the mortality incurred during a moderate winter by several times.

It is concluded that moderate stocking of deer is necessary to maintain the forage yielding capacity of the ranges, soil and watershed values, and in addition, the health and well-being of the herds. It is generally agreed that utilization of the current year's growth of the more palatable browse species should not exceed 60 to 65 percent. The authors believe that stocking on the basis of about 50 percent utilization of the palatable browse on the important deer foraging grounds during moderate winters should result in high sustained forage production and a minimum mortality in severe winters. **Key words: mule deer, mortality, forage quality, snow**

303

Rubin, E. S., W. M. Boyce, and V. C. Bleich. 2000. Reproductive strategies of desert bighorn sheep. Journal of Mammalogy 81(3):769-786. Abstract: We examined temporal breeding patterns of bighorn sheep (*Ovis Canadensis*) in the Peninsular Ranges of California to determine the degree of seasonality and identify potential selection for seasonal breeding in this low-latitude desert environment. During a 4-year period, births occurred during 7 months of the year, but 87% of young were born in February-April and 55% were born in March. Peak months of mating and parturition remained relatively constant across years and among different regions of the Peninsular Ranges, and young born in February through April had greater survival than those born later. Female age influenced lamb survival but not timing of parturition. Successful recruitment of young by an adult female had a weak but significant negative effect on the survival of that female's offspring the following year. Previous reproductive history of a female did not influence offspring production or timing of parturition. Months of peak parturition followed annual winter rains and, therefore, were likely to coincide with periods of high plant productivity. Furthermore, most young were born before the hot, arid summer months. We concluded that bighorn sheep in the Peninsular Ranges are seasonal breeders and that climate patterns likely act as ultimate factors in shaping the breeding season. **Key words: wild sheep, precipitation, temperature, fecundity**

304

Rudd, W. J. 1982. Elk migrations and movements in relation to weather and hunting in the Absaroka Mountains, Montana. Thesis, University of Wyoming, Laramie USA. Abstract: Radio telemetry was used to study migrations and movements of elk (*Cervus elaphus*) in the Absaroka Mountains west of Cody, Wyoming. Movement patterns of elk which migrate from Yellowstone National Park are discussed in relation to hunting and harvest. Resident elk, those that remain east of Yellowstone Park, comprise about 20% of the wintering herd, suggesting their numbers have been reduced during past hunting seasons. Weather patterns influence the timing and magnitude of harvest and migrations were correlated with snow depth. Herd composition data for resident and migrant elk show significantly higher calf production among resident elk. Since the two

herd segments use the same winter ranges, this suggests that summer-fall ranges are an important component to the overall productivity of elk. [The author also states: There was a significant correlation between harvest in previous hunting seasons and precipitation. Fall migrations were less influenced by temperature. While some elk migrated under light snow conditions, most radioed elk migrated in response to approximately 20 cm of snow, which may be a threshold level which induces migration. Elk migrated through much deeper snow at higher elevations to get to winter ranges.] **Key words: elk, snow, movement**

305

Sabine, D. L., S. F. Morrison, H. A. Whitlaw, W. B. Ballard, G. J. Forbes, and J. Bowman. 2002. Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. Journal of Wildlife Management 66(3):718-728. Abstract: White-tailed deer (*Odocoileus virginianus*) exhibit a variety of migration strategies across northern portions of their range. Factors reported as being responsible for migration initiation have shown no consistent pattern. We monitored 186 radiocollared white-tailed deer from 1994 to 1998 in 2 areas of New Brunswick: a southern area with moderate and variable winter climate and a northern area with consistently severe winter climate. We determined that deer in the south contained a large proportion of conditional migrators (individuals that may or may not migrate to winter range in a given year, and may or may not remain until spring), whereas deer in the north consisted almost entirely of obligate migrators (those that annually migrate to winter range for the duration of winter). Occurrence of conditional migration appeared to be a function of climate variability, although distribution of the behavior among individual deer was influenced by migration distance. Initiation of autumn migration in the south was related to snow depth for most deer and represented a response to the proximate cue of the onset of limiting conditions. Autumn migration in the north appeared to be a response to seasonal cues, and the direct influence of snow depth was reduced. Initiation of spring migration in the 2 study areas showed a similar pattern. Migration distance may represent a factor influencing distribution of migrational cues among individual deer within a population. The effect of winter climate variability on deer migration behavior may account for the disparity in behavior reported in the literature. The differences in migration behavior have implications for deer management surveys in northern areas where deer yarding occurs. Managers have assumed that deer observed during winter surveys were on winter range, but this may not be a reasonable assumption in areas with variable winter climates. **Key words: white-tailed deer, migration, snow, census**

306

Sæther, B-E. 1985. Annual variation in carcass weight of Norwegian moose in relation to climate along a latitudinal gradient. Journal of Wildlife Management 49(4):977-983. Abstract: Annual variation in carcass weight during the autumn was studied in four Norwegian populations of moose (*Alces alces*) distributed along a latitudinal gradient (59°N-66°N). In the northernmost population, mean yearling weights were correlated to mean weight of bulls (2 ½ years old) and adult cows ($\geq$3 1/2 years old). Similarly, the mean weight of the calves was correlated with that of yearlings in the southernmost population. In all but one comparison, a combination of climatic variables

explained a significant portion of the annual variation in mean carcass weight. Mean summer temperature, especially the June mean, and summer precipitation were the most important variables. Smaller animals were found in the autumn after a hot rather than a cool summer in the two northern populations. Weather conditions in winter showed little relationship to the annual variation in mean carcass weight. However, a significant relationship was found in the two southern populations, where snow-rich or cold winters were associated with small calves and yearlings in the following autumn. **Key words: temperature, precipitation, moose, morphology**

307

_____ **and A. J. Gravem. 1988. Annual variation in winter body condition of Norwegian moose calves. Journal of Wildlife Management 52(2):333-336.** Abstract: We examined body condition of 40 moose (*Alces alces)* calves shot in winter in southeastern Norway in 1984-85. Kidney fat was low both years. Femur fat was lowest in the year that winter weather was most severe. No relationship between body condition and body weight was found during the severe winter; the relationship was significant during the moderate winter. **Key words: moose, index**

308

Saltz, D., D. I. Rubenstein, and G. C. White. 2006. The impact of increased environmental stochasticity due to climate change on the dynamics of Asiatic wild ass. Conservation Biology 20(5):1402-1409. Abstract: Theory proposes that increased environmental stochasticity negatively impacts population viability. Thus, in addition to the directional changes predicted for weather parameters under global climate change (GCC), the increase in variance of these parameters may also have a negative effect on biodiversity. As a case study, we assessed the impact of interannual variance in precipitation on the viability of an Asiatic wild ass (*Equus hemionus*) population reintroduced in Makhtesh Ramon Nature Reserve, Israel. We monitored the population from 1985 to 1999 to determine what environmental factors affect reproductive success. Annual precipitation during the year before conception, drought conditions during gestation, and population size determined reproductive success. We used the parameters derived from this model to assess population performance under various scenarios in a Leslie matrix type model with demographic and environmental stochasticity. Specifically, we used a change in the precipitation regime in our study area to formulate a GCC scenario and compared the simulated dynamics of the population with a no-change scenario. The coefficient of variation in population size under the global change scenario was 30% higher than under the no-change scenario. Minor die-offs (≥15%) following droughts increased extinction probability nearly 10-fold. Our results support the idea that an increase in environmental stochasticity due to GCC may, in itself, pose a significant threat to biodiversity. **Key words: Asiatic ass, precipitation, drought**

309

Sanford, S. E. 1995. Outbreaks of yersiniosis caused by *Yersinia pseudotuberculosis* in farmed cervids. Journal of Veterinary Diagnostic Investigation 7:78-81. Abstract: Yersiniosis, caused by *Yersinia pseudotuberculosis*,

was diagnosed in 25 deer submitted to the Veterinary Diagnostic Laboratories of the Ontario Ministry of Agriculture and Food from 8 farms in Ontario, Canada, over the 4-year period of January 1990 to December 1993. The organism was cultured, usually in large numbers, from the intestines and, less frequently, mesenteric lymph nodes and/or the spleen of 13 red deer (*Cervus elaphus*), 6 elk (*C. e. canadensis*), 4 fallow deer (*Dama dama*), and 2 red deer-elk hybrids. Outbreaks occurred almost exclusively in the fall (September-November) and affected recently weaned calves, 4-6 months old. Sudden death usually signaled the start of an outbreak. Outbreaks often occurred during inclement weather; usually a sudden cold snap, with or without rain, after a period of relatively mild fall weather. At necropsy, the animals were usually emaciated and dehydrated, and the perineum and tail were sometimes fecally stained. The small and large intestines were congested and filled with serofibrinous and/or seroanguineous fluid. Mesenteric lymph nodes were edematous and congested. Microabscesses surrounding large bacterial colonies in the lamina propria in the jejunum and ileum were typical lesions seen histologically. Peyer's patches were depleted and sometimes contained microabscesses. Purulent lymphadenitis associated with bacterial colonies was the prominent histologic lesion in mesenteric lymph nodes. **Key words: elk, red deer, fallow deer, temperature, precipitation, disease**

310

Sargeant, G. A., L. E. Eberhardt, and J. M. Peek. 1994. Thermoregulation by mule deer (*Odocoileus hemionus*) in arid rangelands of southcentral Washington. Journal of Mammalogy 75(2):536-544. Abstract: Temperature-sensitive, radiotelemetry transmitters were used to measure body temperatures of six free-ranging, adult, female mule deer (*Odocoileus hemionus*) in the semi-arid shrub-steppe of southcentral Washington from 1988 to 1990. Body temperatures ranged from 37.5 to 39.7°C and were similar to rectal temperatures reported for *Odocoileus*. Temperatures followed distinct circannual and circadian patterns unrelated to changes in air temperature or solar radiation. Behavioral thermoregulation may have been important in helping deer avoid thermal stress at environmental temperatures that often exceeded 25°C. On hot, clear days, deer sought beds that provided refuge from solar radiation yet permitted radiative heat loss. **Key words: mule deer, thermoregulation, behavior, temperature**

311

Sauer, J. R. and M. S. Boyce. 1983. Density dependence and survival of elk in northwestern Wyoming. Journal of Wildlife Management 47(1):31-37. Abstract: Survival rates of elk (*Cervus elaphus*) were estimated from tag recovery data. Correlations of yearly survival rates of cow and female calf elk with climatic, hunter kill, and elk population density variables indicate that cow survival varies with climate, but female calf survival changes with both climate and cow population density. Although a variety of climatic, population density, and other environmental factors probably interact to determine elk survival, we could only demonstrate density-dependent survival in calf elk. Age-specific density dependence should be incorporated into models of elk population dynamics to ensure accurate predictions of elk population densities and maximum sustained yields. Severe winters caused decreased survival of both cows and calves. Different components of winter severity affected different age classes, however, with more precipitation early in the winter placing a stress on the juveniles, increasing

early winter mortality. Lower temperatures in midwinter apparently increased cow mortality later in the season. Precipitation in November may also influence mortality by affecting hunter success. Spring and summer climate also seem to exert significant effects on elk mortality. Cow mortality was correlated with temperature in the spring and precipitation in the summer, whereas calf survival (these 'calves' are now yearlings) correlated with temperature in the summer. These patterns may be related to energy stresses associated with reproduction in cows. Inclement weather in summer can lead to decreased energy uptake by elk and result in low energy reserves the next winter. The effects of climate in the spring and summer can cause direct or delayed density-independent mortality. **Key words: elk, temperature, precipitation, mortality**

312

Schaefer, J. A. and W. O. Pruitt, Jr. 1991. Fire and woodland caribou in Southeastern Manitoba. Wildlife Monographs, No. 116. The Wildlife Society, Washington, D.C. Abstract: The effects of fire on the Aikens Lake population of woodland caribou (*Rangifer tarandus caribou*) were studied over a 2-year period. Quantity, quality, and accessibility of forages were determined in recently-burned (5-yr-old) habitats and compared to those in intermediate (37 yrs) and old-growth (90-160 yrs) stands. These measures were correlated with patterns of habitat use by Aikens caribou over 2 winters.

Forage productivity was determined by harvesting the current growth of vascular plants and standing crop of arboreal and terrestrial lichens. Quality of forage was inferred from the contents of acid detergent fiber and published digestibility studies of *Rangifer*. Accessibility of forage was estimated from the Värriö Snow Index, including hardness and thickness of snow cover, and from the intersection frequency of windfallen trees.

Principal components analysis revealed that original floristic distinctions between jack pine (*Pinus banksiana*) and mixed forest communities persisted after fire. Compared to old-growth stands (90 yrs), most burned upland habitats exhibited enhanced productivity of summer forages but a decline in quality and accessibility of winter forages. This deterioration of winter habitat for caribou resulted from the loss of lichens (*Cladina* spp.) in the predominant jack pine communities, the increase in both thickness and hardness of snow cover, and the accumulation of deadfalls. The oldest stands (160 yrs) showed the lowest forage productivity, including lichens, but had the most favorable nival conditions.

Caribou winter travel and feeding were significantly skewed towards use of lakes, old-growth uplands and bogs, and away from burned uplands. In both winters of study, Aikens caribou continued to exploit the remnant lichen supply in old-growth bogs and crown-burned habitats within the limits of the 5-year-old burn. In late winter, however, caribou shifted their activity entirely outside the recent burn in favor of stands $\geq$ 55 years old. The heightened accumulations of snow and deadfalls are implicated in this late-winter range abandonment. The winter range of the population, 5.5 years after fire, was mutually exclusive with its pre-fire range.

Taiga in southeastern Manitoba is not suitable for woodland caribou in its recently-burned and intermediate stages (up to 50 yrs following fire). Yet fire may be necessary to maintain optimal, long-term lichen resources. Due to the remnant lichen supply in burned areas and the delay in the accumulation of windfallen trees, the short-term

detriments of fire may not be fully realized until 5 years or more after burning. Woodland caribou adapt to these short-term effects by abandoning their range. Local fire history — in particular, proximity to alternative, lichen-rich stands — must be considered in the management of woodland caribou habitat. **Key words: caribou, snow, fire, habitat use**

313

Schaller, G. B. and R. Junrang. 1988. Effects of a snowstorm on Tibetan antelope. Journal of Mammalogy 69(3):631-634. Abstract: The authors examined the proximal and long-term impacts of a 1985 blizzard on a population of Tibetan antelope or chiru (*Patholops hodgsoni*). The blizzard deposited about 30 cm of snow, the heaviest on record for the area. Snowfalls on the Tibetan Plateau are generally light, seldom more than 10 cm accumulation, with sun and wind clearing snow within days. In October 1985, however, a heavy snowfall was followed by unseasonable calm and low temperatures (to -40°C and lower). The snow accumulation remained causing animals to expend much energy to obtain little nourishment. The authors visited the area in Qinghai Province in 1985 and 1986. There was no indication of the rut in November 1985. A year later (1986) a pre-rut was evident. The 1985 rut may have been delayed and of low intensity as females failed to enter estrus. There was a small crop of young in 1986. Relatively few male chiru died in 1985 but more females and young, leaving an increased proportion of adult males. A minor vagary in weather caused the death of a significant number of chirus and had a major effect on the population structure. Reproductive success was greatly reduced for a 2-year period and the sex ratio of adults altered markedly. The authors anticipated the single 1985 snowfall would affect the dynamics of the chiru population of the Tibetan Plateau for many years. **Key words: snow, sex ratio, antelope**

314

Schmidt. K. T. and H. Hoi. 2002. Supplemental feeding reduces natural selection in juvenile red deer. Ecography 25:265-272. Abstract: In red deer, variation in winter and spring weather conditions encountered by the mothers during pregnancy and during the first year of life are a main determinant for individual life-history as well as population dynamics. We tested the hypothesis that supplementary feeding which provides constant food supply throughout winter removes the selective pressure of winter harshness on nutrition-mediated phenotypic traits. We analyzed cohort variation in body weight in calves in October, before their first winter, and in yearlings in June, after their first winter, in a food-supplemented population in the Eastern Austrian Alps. Over eleven years, cohort body weight varied between years in calves and yearlings. Contrary to studies on non-supplemented red deer populations we found neither short- nor long-term effects of winter weather on body weight. In calves autumn body weight was negatively related to April-May and June temperatures, suggesting that cool weather during the main growth period retarded plant senescence and thereby prolonged the period of high protein content of summer forage. In yearlings, variation in June body weight, shortly after the end of the feeding period, was lower after a wet April-May, suggesting a negative effect of a prolonged period of supplemental feeding. For both calves and yearlings intra-cohort variation in body weight was higher, inter-cohort variation was lower as compared to non-supplemented red deer, suggesting that in their first year of

life supplemented red deer are under reduced natural selection pressure. **Key words: red deer, nutrition**

315

_____, A. Stien, S. D. Albon, and F. E. Guinness. 2001. Antler length of yearling red deer is determined by population density, weather and early life history. Oecologia 127:191-197. Abstract: In red deer, yearling antler length is a largely nutrition-mediated phenotypic character, and is therefore sometimes used as an indirect estimate of range quality and population condition. However, the parameters affecting yearling antler length have been little studied. We analyze the contributions of density, weather, and maternal effects on yearling antler length of 581 individual stags born 1970-1996 on the Isle of Rum (Scotland). We show that antler length is a good measure of yearling condition: the probability of overwinter survival in yearlings that developed antlers was 3 times higher than for yearlings that did not develop antlers, and yearling antler length was correlated with the number of antler points the following year. Between years, variation in yearling antler length was best explained by variation in red deer density and June temperature at 12 months of age. Both of these variables were negatively correlated with antler length, and most likely this effect is due to changes in nutrient availability. Population density affects biomass availability for the individual, while low temperatures in early summer prolong the availability of high forage quality. At the individual level, antler length increased with birth weight and decreased with birth date, reflecting the persistent and pervasive influence of conditions in early life. **Key words: red deer, index, antler, nutrition, temperature**

316

Schwab, F. E., M. D. Pitt, and S. W. Schwab. 1987. Browse burial related to snow depth and canopy cover in northcentral British Columbia. Journal of Wildlife Management 51(2):337-342. Abstract: Browse from 6 forest sites representing various canopy cover values following logging was marked with 5 color-coded flags in each of 5 0.5-m height zones up to 3.0 m. The proportion of browse buried in each height zone differed significantly ($P<0.001$) among sites at some time during the winter. Stepwise multiple regressions using snow depth and canopy cover as predictor variables indicated that variability in browse burial was predicted best by canopy cover during the snow accumulation period from 3 December to 21 February. During the snow-melt phase (4 Mar-28 Apr) snow depth provided the best prediction of browse burial rates. Increasing browse burial generally corresponded with increasing canopy cover during both the snow accumulation and snow-melt periods. **Key words: snow, diet**

317

Sellers, R. F. and A. R. Maarouf. 1991. Possible introduction of epizootic hemorrhagic disease of deer virus (Serotype 2) and Bluetongue virus (Serotype 11) into British Columbia in 1987 and 1988 by infected *Culicoides* carried on the wind. Canadian Journal of Veterinary Research 55:367-370. Abstract: Outbreaks of epizootic hemorrhagic disease of deer and of bluetongue began in British Columbia in August and October 1987 respectively and recrudescence of infection by both viruses was detected the following year in August. Weather records for up to 18 days before the

initial outbreaks of disease, isolation of virus or seroconversion were examined to determine if the viruses could have been introduced by infected *Culicoides* carried on the wind. Data on temperature, rainfall, wind speed and direction and pressure together with backward trajectory analysis showed that there were suitable winds which could have introduced *Culicoides* infected with epizootic hemorrhagic disease of deer virus on 13 August 1987 (14 days before disease was observed), *Culicoides* infected with bluetongue virus on 1 October 1987 (7 days before virus was isolated and 13 days before disease in sheep) and *Culicoides* infected with bluetongue or epizootic hemorrhagic disease of deer viruses on 20 July 1988 (15 days before seroconversion was detected). The arrival on 13 August 1987 coincided with the passage of a cold front and rain and that on 1 October 1987 with a fall in temperature and calm winds. The source of the *Culicoides* before arrival could have been the Okanogan Valley as far south as the junction of the Okanogan and Columbia rivers in Washington, USA. Flight would have been at temperatures of 12.6°C or higher and at heights up to 1.5 km. **Key words: deer, disease, wind, temperature**

318

Severinghaus, C. W. 1947. Relationship of weather to winter mortality and population levels among deer in the Adirondack region of New York. Transactions of the North American Wildlife Conference 12:212-223. White-tailed deer winter mortality was determined by strip-census between 1930-1946. Deaths mile-1 were compared with temperature and snowfall records. Snow depth and duration was the critical factor affecting winter mortality. Deep snow was more critical late in the season. Depths ≥ 20 inches were critical to deer because a fawn's chest height is 18-19 inches whereas an adult's is 20-22 inches. Sinking depth is the important factor and is influenced by crusts. Deer weaken rapidly when on a restricted range. In the area studied, deep snow must last 5 weeks to significantly affect deer mortality. When the duration exceeds 10 weeks, the effect becomes severe. Temperature is primarily a factor in that it retards snow loss. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver, BC, Canada, pp.50-51.) **Key words: white-tailed deer, snow, mortality**

319

Shannon, N. H., R. J. Hudson, V. C. Brink, and W. D. Kitts. 1975. Determinants of spatial distribution of Rocky Mountain bighorn sheep. Journal of Wildlife Management 39(2):387-401. Abstract: Temporal and spatial distributions of ewe-juvenile groups of Rocky Mountain bighorn sheep (*Ovis canadensis*) in southern British Columbia were studied throughout one annual cycle. With simple and partial correlation analyses, seasonal distribution was related to 11 environmental variables: slope, changes in slope, distance to escape terrain, elevation, aspect, forest cover, shrub productivity, biomass of palatable grasses, nitrogen content of palatable grasses, distance from salt, and snow depth. The influence of individual environmental factors on distribution varied throughout the year. Together the variables accounted for approximately 65 percent of the observed areal variation in counts of bighorn sheep. Mapping of the residuals of the multiple regression equations revealed discrete areas of extreme over- or underestimation. In mid-winter, they [sheep] began to move to slightly higher elevations, occupying open slopes of favorable aspect and exposure. With

greater accumulation of snow, steep rubble slopes, shrub covered slopes, and exposed knolls received heavy use. As snow depth increased in late winter, the animals again moved onto slopes, presumably in response to decreased forage availability. Shrub productivity had little relationship to distribution except during mid-winter when the apparent preference for areas supporting productive shrubs increased dramatically. Several studies have shown that, particularly with heavy snow accumulation, bighorn sheep depend heavily on browse plants. In this study, sheep moved onto lower slopes during this period and were observed to browse extensively, utilizing Saskatoon, willow, rose, and, particularly, redstem ceanothus. **Key words: wild sheep, snow, diet**

320

Shelford, V. E. 1954. The antelope population and solar radiation. Journal of Mammalogy 35(4):533-538. Summary: Based on research in livestock production, Shelford set out to investigate changes in the antelope population in Yellowstone National park in terms of solar radiation and moisture. In Yellowstone the largest populations were associated with rainfall of 11.5 to 15 inches and sunshine of 58 to 65%. Shelford deduced that annual rainfall under 10 inches with September ultraviolet at about 93 is very unfavorable. These conditions were associated with a 46% and 23% decrease of antelope. The author concludes there are sensitive periods in which size of population increase may be determined. Light (UV) appears to be an effective factor influencing fecundity in antelope and probably also milk production. Light is apparently paired with moisture in this regard. **Key words: antelope, fecundity, humidity, solar radiation, precipitation, productivity**

321

Short, H. L., J. D. Newsom, G. L. McCoy, and J. F. Fowler. 1969. Effects of nutrition and climate on southern deer. North American Wildlife Conference 34:137-145. Summary: This study was undertaken to determine if climatic stress and low-quality diet could contribute to the small stature and low densities of white-tailed deer in southern upland forests. High ambient temperatures can directly affect neonate survival. In domestic livestock declines in milk production are noticeable at ambient temperatures near 27°C especially when humidity is high. Food consumption declined at average ambient temperature of 27°C and average relative humidity of 75% for deer. A reduction of food intake at higher temperature, together with an increase in energy expenditure for heat dissipation, may cause reduction or cessation of body growth. The authors state dietary deficiencies in upland habitats probably limit deer numbers as well as weight. Captive does fed deficient diets evidenced substantial fawn losses. High ambient temperatures can directly affect neonate survival. Nutritional stress generally reduces resistance of deer to parasites and disease. **Key words: white-tailed deer, temperature, humidity, nutrition, morphology, density, thermoregulation, disease**

322

Silver, H., J. B. Holter, N. F. Colovos, and H. H. Hayes. 1971. Effect of falling temperature on heat production in fasting white-tailed deer. Journal of Wildlife Management 35(1):37-46. Abstract: Heat production (energy expenditure) of fasting white-tailed deer (*Odocoileus virginianus*) was measured in a respiration chamber at

seven successively lower levels of environmental temperature within the range of approximately 20 to -13 C. Prior to the tests, the deer were fed *ad libitum* on a commercially mixed pelleted ration. They were kept in an outdoor pen, and were acclimated to local weather at the time of the experiments, which were carried out from December to June. They were in thermal equilibrium with the environment at the start of the experiments, but not at subsequent lower levels of chamber temperature. Values calculated for fasting heat production (FHP) per unit of body weight at temperatures in the vicinity of 20 C fit the mouse-to-elephant curve fairly well for deer in winter coat. Corresponding values for deer in summer coat were 70 percent higher. Fasting heat production of a buck clipped in March was 91 percent higher than for full winter coat. Increases in FHP, as ambient temperature fell slightly less than 30° C over a 6-hour period, were relatively greater for deer in summer coats or clipped than for deer in winter coats. At the lowest chamber temperatures, FHP of deer in winter coats was roughly twice the interspecies mean for basal metabolic rate (BMR) of homeotherms; that of deer in summer coats was 3.5 to 5 times the expected basal rate. Seasonal differences appear to be due to the complex interactions of several factors, notably differences in insulating values of summer and winter coats, and probably seasonal differences in pituitary activity. At mean New Hampshire winter temperature, FHP per unit of weight for winter deer was almost the same as that for summer deer at mean summer temperature. It is possible that cyclical physiological changes compensate for seasonal changes in environmental temperature so that energy needs are relatively independent of temperature. **Key words: white-tailed deer, temperature**

323

Sime, C. A., E. Schmidt, and P. E. Farnes. 1998. Acute nutritional stress in white-tailed deer during the 1996/97 winter in northwest Montana. Intermountain Journal of Sciences 4(3/4):92. Abstract (Only): Once every 200-300 years, maximum snow depth at Kalispell Airport reaches that recorded during the 1996/97 winter. Once every 33 years, an equal number of consecutive snow cover days would be recorded. Ungulate overwinter survival depends on many factors, including winter severity and possessing the necessary fat reserves to meet increased thermoregulatory demands and offset nutritional stress caused by low quality forage. To assess the timing and degree of acute nutritional stress in white-tailed deer (*Odocoileus virginianus*), the percent (%) marrow fat content was determined using the oven drying technique for femurs collected from carcasses encountered during field work and along roadways from December 1996 to July 1997. We recorded sex and age, location, cause of death, and death date estimated to Julian week. Cause of death was categorized as vehicle, predation, unknown, or natural (accidents and winter-kill). Percent marrow fat in adult females declined significantly through the winter for vehicle-kills (p=0.0001) but did not decline for those adult females dying of natural causes (p=0.19). In fawns, % marrow fat declined significantly through time for vehicle kills (P=0.008) but not for natural deaths (p=0.66). Fawn natural mortality commenced in late January whereas adult female natural mortality commenced in mid-February. Of those deer which died of natural causes, the marrow fat content averaged 72.4% (95% C.I. 65.7-79.1) for fawns and 66.9% (95% C.I. 58.1-75.8) for adult females. Mean % marrow fat for fawns dying of natural causes was significantly less than for predator-kills (p=0.02), but the difference

was insignificant for adult females (p=0.108). **Key words: white-tailed deer, snow, nutrition**

324

Simpson, D. C., L. A. Harveson, C. E. Brewer, R. E. Walser, and A. R. Sides. 2007. Influence of precipitation on pronghorn demography in Texas. Journal of Wildlife Management 71(3):906-910. Abstract: Ungulate populations in desert environments are thought to be regulated by precipitation. Pronghorn (*Antilocapra americana*) populations in Trans-Pecos, Texas, USA, experienced a 70% decline between 1977 and 2001. The causative factors associated with the decline are unknown but appear to be related to drought. We evaluated the relationships between pronghorn abundance and productivity and precipitation (i.e., raw precipitation, Palmer Drought indices) for the Trans-Pecos district of Texas from 1977 to 2004. Pronghorn productivity (range=305-4,407) and abundance (range=5,061-17,266) showed high variability. Precipitation was also highly variable, ranging from 18 cm to 57 cm. Pronghorn abundance was positively influenced by precipitation indices (R=0.790, P<0.001). The relationship between fawn production and raw precipitation (R=0.869, P<0.001) suggested that fawn production may be more closely related to immediate moisture conditions, whereas pronghorn abundance was more influenced by long-term population trends. Management plans for pronghorn populations in more arid regions should include drought contingencies including reduced stocking rates and harvest quotas. **Key words: antelope, drought, precipitation, population dynamics**

325

Sims, M., D. A. Elston, A. Larkham, D. H. Nussey, and S. D. Albon. 2007. Identifying when weather influences life-history traits of grazing herbivores. Journal of Animal Ecology 76:761-770. Summary: 1. There is increasing evidence that density-independent weather effects influence life-history traits and hence the dynamics of populations of animals. Here, we present a novel statistical approach to estimate when such influences are strongest. The method is demonstrated by analyses investigating the timing of the influence of weather on the birth weight of sheep and deer. 2. The statistical technique allowed for the pattern of temporal correlation in the weather data enabling the effects of weather in many fine-scale time intervals to be investigated simultaneously. Thus, while previous studies have typically considered weather averaged across a single broad time interval during pregnancy, our approach enabled examination simultaneously of the relationships with weekly and fortnightly averages throughout the whole of pregnancy. 3. We detected a positive effect of temperature on the birth weight of deer, which is strongest in late pregnancy (mid-march to mid-April), and a negative effect of rainfall on the birth weight of sheep, which is strongest during mid-pregnancy (late January to early February). The possible mechanisms underlying these weather-birth weight relationships are discussed. 4. This study enhances our insight into the pattern of the timing of influence of weather on early development. The method is of much more general application and could provide valuable insights in other areas of ecology in which sequences of intercorrelated explanatory variables have been collected in space or in time. **Key words: deer, sheep, birth weight, temperature, model**

326

Singer, F. J. 1979. Habitat partitioning and wildlife relationships of cervids in Glacier National Park. Journal of Wildlife Management 43:437-444. Summary: Snow depth was the key factor determining habitat partitioning by moose, elk, and white-tailed deer. Open types had the most snow (mean=80 cm) whereas Douglas-fir forests had the least (mean=12 cm). Moose were more often found in open types whereas deer were more often in the dense Douglas-fir forest. All three species also utilized the spruce forest with intermediate snow depths (mean=40 cm). (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography,* University of BC, Vancouver, BC, Canada, pp. 51=52.) **Key words: moose, elk, white-tailed deer, snow, distribution**

327

_____, A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management 61(1):12-25. Abstract: We studied survival of radiocollared elk (*Cervus elaphus*) calves in Yellowstone National Park from 1987 to 1990, and survival of calves computed from population estimates from 1968 to 1992. We hypothesized that summer and winter survival of elk calves and mass of neonates were inversely related to population size, measures of environmental severity, and timing of births. Herd-wide survival estimates based on winter counts, reported harvests, and herd classifications, suggested that winter survival of elk calves was related inversely to estimated size of the elk population during winter (P=0.0002), but we found no correlation with an index of winter severity (P=0.51). Summer survival of elk calves also was correlated inversely with the estimated size of the elk population the previous winter (P=0.03). Summer survival of radiocollared calves averaged 0.65 (n=127 marked calves) from 1987 to 1990, the losses mostly due to predation (22%). Winter survival of calves averaged 0.72 (n=88 marked calves entered the winter period), with losses due mostly to malnutrition (58%). Summer survival of radiocollared calves was positively correlated with estimated birth weight (P=0.001). Survival of radiocollared calves during winters 1987-90 was correlated positively with early calving and mildness of the winter (in contrast to herd-wide survival estimates), and was inversely correlated with estimated elk population size that winter (P=0.006). Winter survival of radiocollared calves was lower during 1988-89 following the drought and large fires than the other 3 winters (P<0.001). Predation on elk calves during summer doubled after the drought and fires of 1988 (13% calf losses to predation before the fires vs. 29% after the fires). Potential compensation existed between components of calf mortality; predators killed more light (P=0.041) and more late born calves (P=0.146); calves were born later and lighter (P=0.048) following severe weather conditions; and heavier born calves survived at a higher rate (P=0.006). Our results are consistent with the hypothesis that density-dependent mortality of calves during winter due to malnutrition, and summer mortality of calves due to additive components to both summer (increased predation) and winter (increased malnutrition) mortality. **Key words: elk, mortality, drought, fire**

328

_____, W. Schreier, J. Oppenheim, and E. O. Garton. 1989. Drought, fires, and large mammals: evaluating the 1988 severe drought and large-scale fires. BioScience 39(10):716-722. Abstract: Drought and above-average winds led to extremely dry conditions and subsequent fires in Yellowstone in 1988. The fire resulted in a low mortality rate (1%) among elk. Dead mammals were found in sites of sustained wind speeds of 10-20 kph with gusts of 60 kph during the fires. Elk moved onto winter range 4-6 weeks early in apparent response to drought and fire. 54% of the northern elk herd left the park. This movement was thought to be in response to effects of drought and fire on forage and a subsequent heavy snowpack. Bull elk died at higher rates than cows due to staying in burned and high snow areas. Calf elk experienced high winter mortality, dropping from 20:100 cows to 7:100 cows. Although mule deer and antelope winter range escaped the fires, drought and winter conditions led to a decline of 19% for mule deer and 29% for antelope. The following year calf elk mortality was twice that of the previous year and calf weights were reduced 17%. The combined effects of drought and fire was a large die-off the following winter. **Key words: elk, mule deer, antelope, bison, drought, fire, wind, movement, snow, sex ratio, mortality**

329

Skogland, T. 1978. Characteristics of the snow cover and its relationship to wild mountain reindeer (*Rangifer tarandus tarandus* L.) feeding strategies. Arctic and Alpine Research 10(3):569-580. Abstract: Snow profiles were sampled along an east-west gradient in wild reindeer home range from winter ground in the east to calving ground in the west. Hardness to ramsonde at Finse (west) increased from 22 to 395 kg from early to late winter; hardness in the winter habitat (east) increased from 40 to 140 kg in cratered areas (p<0.01, t-test between west, uncratered and cratered areas). Density increased from 0.20 to 0.37 g cm $^{-3}$ in early winter to 0.40 to 0.55 g cm $^{-3}$ in late winter prior to melt off (p<0.01, t-test between areas). Hardness measured with the spring penetrometer increased from 200 to 400 g cm $^{-2}$ in late winter prior to melt off in cratered areas. The ramsonde was used to measure the wind-hardened snow and the spring penetrometer to measure soft snow.

Pawing rate (strokes per minute) decreased linearly with increasing density (Y=0.54X+20.3, r=0.96, p<0.01) and exponentially with hardness (g cm^{-2})(Y=52.7-6.94 1n X, r=0.92, p<0.01). Significantly different smilogarithmic relationships between density and hardness were found in cratered areas and in uncratered areas. Wind-hardening influenced snow structure more in uncratered than cratered areas. Crater depths decreased inversely with increasing density (Y=-8.08 – 22.86 1n X, n=8, r=0.8, p<0.01; and hardness, Y=61.23-7.58 1N X, r=0.83, p<0.01) restricting reindeer to the upper zone of the *Loiseleurio-Arctostaphylion* heaths. Collapse of snow structure in May in the low alpine zone was the major factor accounting for reindeer movement into the middle alpine zone where there was a supportive snow cover but more restricted grazing areas. **Keywords: reindeer, snow, behavior**

330

Smith, B. L. 1998. Antler size and winter mortality of elk: effects of environment, birth year, and parasites. Journal of Mammalogy 79(3):1038-1044. Abstract: Correlates with antler size of 215 male elk (*Cervus elaphus*) that died during 5 winters on the National Elk Refuge, Wyoming, were investigated. The elk were 1.5-14.5 (mean=6.5, SE=0.19) years old. Males with clinical infestations of scab mites (*Psoroptes*) had antlers with more points, greater beam circumference, and greater mass than males not afflicted with mites. Development of antlers and infestation with scabies were correlated positively with age. Controlling for age, antler size was correlated with March and April temperatures during the year that they grew (nutritional effect) and weather conditions while the males were *in utero*. Population size, adult sex ratio, and supplemental winter feeding of elk at the National Elk Refuge exhibited no apparent influences on antler size. **Key words: elk, antlers, nutrition**

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_____ **1977. Influence of snow conditions on winter distribution, habitat use, and group size of mountain goats. Proceedings of the International Mountain Goat Symposium 1:174-189.** Abstract: Habitat relationships of mountain goats (*Oreamnos americanus*), native to the Bitterroot Mountains of western Montana, were studied from January 1973 to June 1975. Distribution and habitat use on winter ranges were evaluated in terms of elevation, exposure, slope inclination, terrain types, vegetative associations, and size of winter range used by goats. Observed variations during and between three winters were related to snow conditions. When snow depths were greatest, lower elevations, southern exposures, and cliff terrain were used a greater percentage of the time. Mean group size declined and amount of winter range occupied increased during two severe winters versus a mild winter. Adult females exploited snow-free portions of cliffs while subdominants used less optimum habitat. Successful exploitation of optimum habitat, where energy expenditures are minimized, likely promotes survival of females and their offspring. **Key words: mountain goat, snow, distribution, habitat use, population dynamics**

332

Smith, D. R. 1954. The bighorn sheep in Idaho: its status, life history and management. Wildlife Bulletin No. 1, Idaho Department of Fish and Game, Boise. Notes: In Part I, Bighorn Habitat the author notes the following: “The most satisfactory means for judging the consequences of weather on game populations is by direct observation of conditions in the field. The amount of snow present is not as important as the condition of the snow. A heavy crust may render large areas of range unavailable. The degree and duration of this crust, as well as the temperature and depth of snow, determine the severity of a winter. It is on winter ranges during winter and early spring that weather becomes a particularly significant factor in the bighorn’s odds for survival. There is, of course, a very important relationship between precipitation and temperature and the development of forage….Differences in precipitation and other climatic conditions influence the annual production of forage and this must be taken into consideration if utilization measurements are to be applied realistically as a factor for

determining carrying capacity. **Key words: wild sheep, snow, ice, temperature, nutrition, precipitation**

333

Smith, R. H. and A. Lecount. 1979. Some factors affecting survival of desert mule deer fawns. Journal of Wildlife Management 43(3):657-665. Abstract: This 9-year study found a strong association (*n*=0.94) between aggregate rainfall on the Three Bar Wildlife Area during October-April and forage yield from forbs and small shrubs as measured in April. Survival of mule deer fawns (*Odocoileus hemionus crooki*) as reflected in the ratio of fawns per 100 does during January was also strongly associated with winter forb yield (*r*=0.83) and October-April rainfall (*r*=0.64) of the winter-spring period preceding the fawning period. A small herd of deer within a 244-ha predator-proof enclosure on the same area had significantly higher average January ratios of fawns:100 does than the herd outside of the enclosure. The ratios (1972-78) were not associated with forb production. These results suggest that forage condition, except in years with extreme winter drought, is probably not the factor that is limiting fawn survival in the herd outside of the enclosure to its present low levels. **Key words: mule deer, precipitation**

334

Solberg, E. J., M. Heim, V. Grøtan, B-E Sæther, and M. Garel. 2007. Annual variation in maternal age and calving date generate cohort effects in moose (*Alces alces*) body mass. Oecologia 154(2):259-271. Abstract: A general feature of the demography of large ungulates is that many demographic traits are dependent on female body mass at early ages. Thus, identifying the factors affecting body mass variation can give important mechanistic understanding of demographic processes. Here we relate individual variation in autumn and winter body mass of moose calves living at low density on an island in northern Norway to characteristics of their mother, and examine how these relationships are affected by annual variation in population density and climate. Body mass increased with increasing age of their mother, was lower for calves born late in the spring, decreased with litter size and was larger for males than for female calves. No residual effects of variation in density and climate were present after controlling for annual variation in other age and calving date. The annual variation in adult female age structure and calving date explained a large part (71-75%) of the temporal variation in calf body mass. These results support the hypotheses that (a) body mass of moose calves are affected by qualities associated with mother age (e.g. body condition, calving date); and (b) populations living at low densities are partly buffered against temporal fluctuations in the environment. **Key words: moose, density, parturition**

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_____, P. Jordhøy, O. Strand, R. Aanes, A. Loison, B-E Sæther, and J. D. C. Linnell. 2001. Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. Ecography 24:441-451. Abstract: To determine the main factors affecting the population dynamics of Svalbard reindeer, we analyzed 21 yr of annual censuses, including data on population size, recruitment rate (calves per female) and mortality (number of deaths), from the Reindalen reindeer population. In

accordance with previous studies on population dynamics of Svalbard reindeer, we found large inter-annual variation in population size, mortality and recruitment rates within the study area. Population size decreased in years with low recruitment rate as well as high winter mortality and vice versa. Apparently, the fluctuations were due to both direct density-dependent food limitation and variation in winter climate associated with high precipitation and icing of the feeding range. We found no delayed density-dependence or effect of climatic conditions during summer on the population dynamics. The mortality during die-off years was mainly of calves and very old individuals, indicating that the population was more vulnerable to high die off in years following high recruitment rate. These results suggest an unstable interaction between the reindeer population and its food supply in these predator-free environments. **Key words: caribou, precipitation, ice, mortality**

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_____, B-E. Sæther, O. Strand, and A. Loison. 1999. Dynamics of a harvested moose population in a variable environment. Journal of Animal Ecology 68:186-204. Abstract: 1. Population size, calves per female, female mean age and adult sex ratio of a moose (*Alces alces*) population in Vefsen, northern Norway were reconstructed from 1967 to 1993 using cohort analysis and catch-at-age data from 96% (6752) of all individuals harvested. 2. The dynamics of the population were influenced mainly by density-dependent harvesting, stochastic variation in climate and intrinsic variation in the age-structure of the female segment of the population. 3. A time delay in the assignment of hunting permits in relation to population size increased fluctuations in population size. 4. Selective harvesting of calves and yearlings increased the mean age of adult females in the population, and, because fecundity in moose is strongly age-specific, the number of calves per female concordantly increased. However, after years with high recruitment, the adult mean age decreased as large cohorts entered the adult age-groups. This age-structure effect generated cycles in the rate of recruitment to the population and fluctuations introduced time-lags in the population dynamics. 5. An inverse relationship between recruitment rate and population density, mediated by a density-dependent decrease in female body condition, could potentially have constituted a regulatory mechanism in the dynamics of the population, but this effect was counteracted by a density-dependent increase in the mean age of adult females. 6. Stochastic variation in winter snow depth and summer temperature had delayed effects on recruitment rate and in turn population growth rate, apparently through effects on female body condition before conception. **Key words: moose, temperature, snow**

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Staines, B. W. 1976. The use of natural shelter by red deer (*Cervus elaphus*) in relation to weather in north-east Scotland. Journal of Zoology, London 180:1-8. Abstract: The use of natural shelter in relation to weather by red deer on open moorland is described. Most shelter-seeking behavior in winter was associated with the chilling effects of wind. Although deer sheltered from both wind speed and temperature individually, the combined effect of these (i.e. “windchill”) was likely to be most important. The most important individual factor was wind. In winter, resting deer sheltered from the wind by lying on lee slopes, in long vegetation, on dry ground and in places with small amounts of geomorphic shelter; they sought very sheltered places only during blizzards.

Deer were found in more shelter as windchill increased, and did not appear to seek constant conditions from day to day. They put up with worse conditions when feeding than when resting. On summer days with high temperatures and strong sun, deer were seen standing when at rest, and were found in the shade, and on wet or bare ground; they also lay in the wind, bathed in water or stood on patches of old snow. **Key words: red deer, wind, behavior**

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Stenseth, N. Chr. and A. Mysterud. 2005. Weather packages: finding the right scale and composition of climate in ecology. Journal of Animal Ecology 74:1195-1198. Summary: 1. Animals are affected by local weather variables such as temperature, rainfall and snow. However, large-scale climate indices such as the North Atlantic Oscillation (NAO) often outperform local weather variables when it comes to explain climate-related variation in life history traits or animal numbers. 2. In a recent paper, Hallet *et al* (2004 *Nature*, 430, 71-75) document convincingly why this may happen. In this perspective, we identify from the literature three mechanisms why this is so: (1) the time window; (2) the spatial window; and (3) the weather composition component of climate. 3. Such an understanding may be used to derive even better 'weather packages' than the NAO. **Key words: NAO**

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Stephenson, T. R., V. Van Ballenberghe, J. M. Peek, and J. G. MacCracken. 2006. Spatio-temporal constraints on moose habitat and carrying capacity in coastal Alaska: vegetation succession and climate. Rangeland Ecology & Management 59(4):359-372. Abstract: We used a geographic information system and a Markov chain analysis to model vegetation succession on the Copper River Delta, Alaska, relative to moose (*Alces alces*) habitat availability and nutritional carrying capacity. Between 1959 and 1986 vegetation predominantly shifted from pioneer to later successional communities as a result of glacial retreat and earthquake uplift. Hypothesized vectors of vegetation composition in future decades indicate a trend toward an increase in late-successional communities. A decline in glacier-related disturbance has reduced the level of retrogression that maintains early successional communities in the outwash plain. In addition, landscape heterogeneity increased significantly between 1959 and 1986, particularly in the uplifted marsh. Winter severity was highly variable among years and was correlated with a shift in the location of moose wintering areas. As winter severity increased, there was increased use of the glacial outwash plain landform and its associated plant communities. Successional modeling suggests a decline in the availability of vegetation types important to moose during severe winters with deep snow. Low willow (*Salix* spp.) communities are expanding in the uplifted march, a landform used primarily during summer and mild winters. However, tall willow communities that provide winter forage are declining and are being replaced by Sitka spruce (*Picea sitchensis* [Bong] Carr) forest in the glacial outwash plain. Consequently, nutritional carrying capacity of moose on the outwash plain during winter will decline by 42% during 1959-2013. **Key words: moose, habitat use, diet**

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Stevens, D. and A. N. Moen. 1970. Functional aspects of wind as an ecological and thermal force. Transactions North American Wildlife and Natural Resources Conference 35:106-114. Summary: Heat transfer on the thermal surface of an animal is a dynamic process affected by wind which penetrates the hair, disturbs the insulating hair layer and alters the surface temperature and temperature profile changes in the orientation of the hair and other biological responses contribute to variation in the thermal parameters. Wind flow patterns are extremely variable, being influenced by vegetation, topography and the animal surface itself. Care must be taken to properly identify the wind flow characteristics and their effect on the thermal surface of the animal before attempting to use remote sensing to detect different animal species by their surface thermal characteristics. **Key word: wind, technique**

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Stewart, S. T. 1982. Late parturition in bighorn sheep. Journal of Mammalogy 63(1):154-155. Notes: The author notes a late parturition of bighorn sheep on the West Rosebud range of Montana. He states this unusual lateness may represent an adaptation to climatic conditions unique to the area. Sheep migrated to open southeast facing slopes at lower elevations for spring “green-up” that is as late as April 15 to May 1. Severe snowstorms occur frequently in May, further restricting availability of new growth vegetation. A high quality diet is not assured until mid-May. **Key words: wild sheep, snow, parturition, diet**

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Swanson, B. J. 1998. Autocorrelated rates of change in animal populations and their relationship to precipitation. Conservation Biology 12(4):801-808. Abstract: I examined the prevalence of autocorrelation in mammalian, avian, and precipitation time series, how well autocorrelation in the environment translates into autocorrelation in animal populations, and length of the time series needed to accurately characterize the degree of autocorrelation. These are important questions because more-complex population models are incorporating autocorrelation terms in life-history characteristics and the intrinsic rate of increase. Including inaccurate or nonsignificant autocorrelation can alter the conclusions reached, providing either an unduly rosy or bleak picture of the likelihood of population viability and persistence. Using autocorrelation analysis in 175 vertebrate and 88 precipitation data sets, I found that 17.8% of the mammalian time series, 61.5% of the avian time series, and 97.7% of the precipitation data sets were autocorrelated. Carnivore populations were more likely than herbivore populations to show significant autocorrelation at lags of 2 or more years. I found only two cases of significant cross correlation between rate of population increase and local precipitation. This indicates that, although some environmental variables may be highly autocorrelated, it does not translate into autocorrelation in the resident animal populations. Based on subsampling of the precipitation and vertebrate data, I found that 15 years of data is sufficient to produce an autocorrelation not significantly different from one based on 100 years of data, although the variance continues to decrease with the length of the time series, as expected. My results suggest that, although some populations show temporal autocorrelation, it is not ubiquitous, and that environmental

autocorrelation may not be a good predictor of autocorrelation in rates of increase. Population modelers should determine if autocorrelation exists in populations of interest prior to modeling their viability or probability of persistence because not all populations are equally influenced by autocorrelation. **Key words: precipitation, model**

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Sweeney, J. 1975. Elk movements and calving as related to snow cover. PhD thesis, Colorado State University, Fort Collins, CO. Snow depths of 30 cm did not impair the mobility of elk whereas greater depths produced movements to areas with less snow. Elk can paw through only about 40 cm of snow. Physical limitations in movement (critical depth) occur at about 70 cm. Discusses interactions between depth and hardness. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography,*University of BC, Vancouver, BC, Canada, p. 53.) **Key words: elk, snow, distribution, movement**

344

Sweeney, J. M. and J. R. Sweeney. 1984. Snow depths influencing winter movements of elk. Journal of Mammalogy 65(3):524-526. Abstract: The objective of this study was to determine those snow depths which influence elk winter movements. Establishment of specific snow depth criteria will permit the development of winter range habitat use models for subsequent incorporation into integrated resource systems. Monthly snow depths (dm) were recorded at 31 sites, to provide an estimate of the overall snow pattern on the study area. At each site, five or nine snow stakes were deployed systematically over a 10-m^2 area.

Thirty-three aerial surveys during the four winter seasons produced 1,262 sightings of elk. These sightings indicated that the initiation and pattern of elk movements were regulated by snow cover. All 1970-71 winter sightings of elk were in areas with less than 35 cm of penetrable snow cover. Throughout the following three winter seasons, elk were most often located in areas with less than 40 cm of penetrable snow when such areas were available. With the exception of one elk in December 1971, the only sightings of elk in areas with greater than 70 cm of penetrable snow were during the severe winter of 1972-73.

Data from this study indicated that elk movement patterns were keyed to at least two different snow depths, 40 and 70 cm; both depths resulted in elk moving to areas with less snow. Snow depths of less than 40 cm apparently did not physically impair the mobility of elk; but snow depths approaching 40 cm did cause elk to move to areas with less snow. During the four winter seasons studied, evidence of elk pawing through snow to obtain food was observed only where grasses and forbs extended above the snowpack. This was usually in areas with less than 40 cm snow depth. The movement response to the 40-cm depth may be a behavioral response keyed to feeding habits.

The 40-cm response depth was not a critical maximum. Sites with greater than 70 cm snow depth were, however, rarely utilized.

These two snow depths, the 40-cm response depth and the 70-cm critical depth, can be used in winter habitat use models to calculate available winter range under varying snow conditions. **Key words: elk, snow, behavior**

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Taber, R. D. 1958. Development of the cervid antler as an index of late winter physical condition. Proceedings of the Montana Academy of Sciences 18:27-28. Abstract: Experiments have shown that diet has an effect on the ultimate size and development of antlers. One study found that mature stags produced well developed antlers only when they were at the peak of physical condition before as well as during antler growth. Another found that those fed diets deficient in quantity, protein or protein and minerals showed body weight gain and especially antler development far inferior to those fed diets adequate in quantity and quality. The authors found that 2-year-old bucks switched from a diet of low quality to high quality about two weeks before the start of antler growth in spring developed antlers less than half as heavy as those maintained on a complete diet throughout the study. A study in Allegheny National Park Pennsylvania showed yearling bucks in a population stressing its range decreased antler volume by 50%. Yearlings display a greater degree of antler stunting under the same range conditions experienced by adult bucks.

Taber speculates that antler development, especially in yearlings, may prove to be a useful indicator of physical condition of the animal at the time antler growth began. Measurement of antler development during the hunting season might be a reflection of dietary level of the animals the previous winter. Thus, antler studies may prove to be a valuable supplement to studies of the winter range for cervids. **Key words: deer, antler, index, forage quality**

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Taillon, J., D. G. Sauvé, and S. D. Côté. 2006. The effects of decreasing winter diet quality on foraging behavior and life-history traits of white-tailed deer fawns. Journal of Wildlife Management 70(5):1445-1454. Abstract: Many high-density populations of wild ungulates have exerted strong negative impacts on their habitat. A decrease in forage quantity and quality may affect individual growth, fecundity, and survival, especially under harsh winter conditions. On Anticosti Island, Quebec, Canada, browsing by introduced white-tailed deer (*Odocoileus virginianus*) negatively affected boreal forest composition. Since the preferred contemporary winter forage of deer, balsam fir (*Albies balsamea*), had been almost completely extirpated from the island at browse height, deer are forced to increase the proportion of normally avoided forage, such as white spruce (*Picea glauca*) in their winter diet. We predicted that an increase in the proportion of white spruce in the diet would have detrimental effects on deer body condition and would affect their behavior and life-history traits. We experimentally simulated a deterioration of winter forage quality in semi-natural enclosures by increasing the proportion of white spruce in the diet and examined the effects of winter diet quality on 1) forage intake, 2) body condition loss, 3) activity budget, and 4) survival of white-tailed deer fawns. Fawns fed the poor-quality diet maintained a higher forage intake rate throughout the winter than fawns fed the control diet, suggesting a compensatory response to the decrease of forage quality by consuming more forage during winter. Body mass decreased over the winter, but we did not observe any significant effects of diet quality on body mass loss. Diet quality did not influence the activity budget of fawns, but deer decreased activity in cold weather. The main determinant of overwinter survival was individual body mass in early winter. Our study suggests that deer have adapted to the extreme conditions encountered on Anticosti

(i.e., harsh and long winters, low-quality browse, and a high-density population). Even though white spruce stands are gradually replacing balsam fir stands, our results suggest that deer on Anticosti could maintain a high-density population by increasing the amount of white spruce in their diet. However, future studies are necessary to address the long-term effects of a diet dominated by white spruce on deer body condition, survival, and reproduction under natural conditions. **Key words: white-tailed deer, diet**

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Takatsuki, S. 1992. Foot morphology and distribution of sika deer in relation to snow depth in Japan. Ecological Research 7(1):19-23. Abstract: The distribution of Sika deer (*Cervus nippon*) on Japanese islands is biased toward the east where there is less snow. To explain this biased distribution in relation to snow, the foot morphology of Sika deer was measured. Hoof load was greatest in male adults (0.78 kg cm-2) and smallest in fawns (c. 0.43 kg cm-2). The values were similar to those for white-tailed deer, and were smaller than those for snow-adapted species like caribou and chamois. Foreleg length was c. 50 cm and 60 cm, and hind feet (lower half) length was c. 40 cm and 45 cm for fawns and adult deer, respectively. Chest heights were c. 45 cm and 53 cm for fawns and adults, respectively. These figures suggest that areas where snow accumulates deeper than 50 cm are not favorable as a Sika deer habitat. The present distribution of Sika deer is clearly related to snow depth: they are mostly concentrated in the 'preferable area' of <50 cm of snow, some of them can live in the 'habitable area' of 50-100 cm of snow, and they rarely live in the 'inhabitable area' of >100 cm of snow. **Key words: Sika deer, snow, distribution, morphology**

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Taper, M. L. and P. J. P. Gogan. 2002. The northern Yellowstone elk: density dependence and climatic conditions. Journal of Wildlife Management 66(1):106-122. Abstract: We analyzed a time series of estimates of elk (*Cervus elaphus*) numbers on the northern Yellowstone winter range from 1964 to 1979 and 1986 to 1995 using a variety of discrete time stochastic population dynamic models. These models included adjustments for density, an increase in the area of winter range used by elk, lagged effects of the weather covariates of spring precipitation, snow depth and winter temperature, and the impacts of the 1988 drought and fires. An information-criteria-based model-selection process strongly supported evidence of density dependence. The best model, a Ricker model, distinguished between the 2 time periods. The bulk of the difference between the 2 periods is attributed to an increase in the amount of winter range used by elk. Inclusion of the covariates spring precipitation and spring precipitation squared greatly improved the model fit. We detected a short-lived increase in elk population growth rate following the 1988 drought and fires. Fertility and survivorship of adults appeared to have different density-dependent forms that together result in a biphasic relationship between population growth rate and density. This study confirms the presence of density-dependent regulation in the northern Yellowstone elk herd, and enhances our understanding of population dynamics of these ungulates. **Key words: elk, population dynamics, precipitation, temperature**

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Taylor, S. and K. Brunt. 2007. Winter habitat use by mountain goats in the Kingcome River drainage of coastal British Columbia. BC Journal of Ecosystems and Management 8(1):32-49. Abstract: using radio telemetry from September 1994 to March1996, we studied the winter habitat use of 15 mountain goats in the Kingcome River drainage on the south coast of British Columbia, Canada. Our objectives were to identify important attributes of coastal mountain goat winter habitat and, in doing so, to provide resource managers with information that will help them make decisions about conserving and managing goat habitat in coastal British Columbia. We used a digital elevation model, Terrestrial Ecosystem Mapping, and Vegetation Resource Inventory mapping with a Geographic Information System to determine selection by 13 female mountain goats for forested site series and other habitat variables at two different scales. At both scales of selection, mountain goats chose southerly aspects (110-250°) and western hemlock-leading forests greater than 250 years in age, but we observed no evidence for site series preference. Most goat locations were within 150 m distance of rock-outcrop polygons. Depending on the scale of selection analyses, goats selected elevations from 600-1200 m, slopes from 41 to 60°, and the Montane Very Wet Maritime Coastal Western Hemlock (CWHvm2) or Windward Moist Maritime Mountain hemlock (MHmm1) subzone variants. Goats selected moderate classes of forest volume and crown closure, and sites with shrub cover 1-2 m in height. These attributes are likely associated both with lower snow depths and higher amounts of available forage for goats. Our study shows that it is important for managers to assess whether planned harvests conflict with goat winter habitat. Although the harvestable area on the coast that overlaps with goat winter habitat may not be large, some of these habitats could be very important for goats, particularly during deep snow periods. **Key words: mountain goat, snow, habitat use**

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Taylor, W. P. and H. C. Hahn. 1947. Die-offs among the white-tailed deer in the Edwards Plateau of Texas. Journal of Wildlife Management 11(4):317-323. Summary: A drought during the late summer and early fall of 1942 reduced succulent foods on the Texas range. In addition to large deer populations, large numbers of domestic stock were simultaneously grazing the range. As a result of severe competition for food, the deer were in a weakened condition and the onset of a cold month in October increased mortality. As a result of their weakened state, many deer experienced secondary infections which result in death including stomach worms, ticks, screw worms, and pneumonia. Most deaths occurred among yearling does and fawns with a reduced rate among bucks. **Key words: white-tailed deer, nutrition, drought, disease, mortality, temperature**

351

Teer, J. G., J. W. Thomas, and E. A. Walker. 1965. Ecology and management of white-tailed deer in the Llano Basin of Texas. Wildlife Monograph 15, the Wildlife Society. Summary: In the Llano Basin and Edwards Plateau precipitation is the chief factor regulating carrying capacity of the rangelands, and population densities of deer fluctuate about the carrying capacity in response to the interaction of the herd with its

food supply. Population densities of deer in the Basin were related to the mean annual precipitation in the preceding year. This relationship was very close during the years of the drought (1953-1956), but loosened after precipitation increased to average or above-average amounts. Population densities were reduced drastically during the drought, and remained low until 1958. During the first year that precipitation approached the long-term average, the deer herd increased the following year. After the drought ended in 1957, the herd began to increase without interruption despite minor fluctuations in annual precipitation. However, at no time during the above-average period did rainfall drop below the long-term average. The relationship of population densities to precipitation in the preceding year was partially imposed by the breeding cycle of the herd. Physical condition of the deer at the time of the rut in the fall influences reproductive rates, but the increment to the herd occurs the following year. A delay in response and recovery of range vegetation to changes in precipitation seems to be a chief reason for the lag in fluctuations in deer numbers. In summary, carrying capacities of the rangelands of the llano Basin and the Edwards Plateau for deer decrease from east to west, and precipitation is the ecological factor regulating carrying capacity and population densities of deer. Annual precipitation regulates the density of plants and forage production on which herbivores depend. Asymptotic levels of numbers of deer are determined primarily by mean annual precipitation through its influence on vegetation. Fluctuations in numbers of deer around these asymptotic levels are related to changes in annual precipitation. **Key words: white-tailed deer, precipitation, drought, nutrition, fecundity, density**

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Telfer, E. S. 1978. Cervid distribution, browse and snow cover in Alberta. Journal of Wildlife Management 42(2):352-361. Abstract: Studies of winter distribution of moose (*Alces alces*), elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) were conducted in the Montane Forest Region of southwestern Alberta, the Mixedwood Section of the Boreal Forest of central Alberta and the Upper Foothills Section of the Boreal Forest Region in west central Alberta. Pellet-group counts supplemented by aerial and ground observation showed that moose utilization of study areas was positively related to the weight of winter browse per unit area. Elk and deer winter utilization was not strongly related to browse availability, but may be related to traditional wintering areas and to human disturbance. The integrity of traditional winter range, especially steep south-facing slopes of major drainages and bottoms of large valleys should be maintained as essential winter habitat for deer and elk in the foothills. Moose distribution can be altered and populations possibly increased by manipulating browse supply. **Key words: deer, moose, distribution, snow**

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_____.1967. Comparison of moose and deer winter range in Nova Scotia. Journal of Wildlife Management 31(3):418-425. In Nova Scotia, deer retreated from the highlands in winter whereas moose did not. Mean winter snow depths and densities showed no differences between deer and moose areas, although April snow depths were much greater in the moose area. The moose area had 30 inches of snow, an amount thought unlikely to hinder moose. In the spring, deer moved to deep snow areas to feed early on cold mornings but returned before the sun softened the crust. The lack

of association between deer and moose in winter may hinder the transmission of *Pneumostrongylus tenuis* ("moose sickness"). (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver, BC, Canada, p. 53.) **Key words: white-tailed deer, moose, snow, distribution, movement**

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_____ **and J. P. Kelsall. 1979. Studies of morphological parameters affecting ungulate locomotion in snow. Canadian Journal of Zoology 57:2153-2159.** Body weight, chest height, and various hoof measurements were made on moose, wapiti, white-tailed deer, and bison carcasses obtained in slaughter reductions in Elk Island and Jasper National Parks, Alberta. The separation in chest heights of fully mature deer, wapiti, and moose suggests a morphological adaptation to resource partitioning based on differential ability to exploit various snow depths. White-tailed deer exhibit the smallest foot-loading; male bison the greatest. There are significant sex differences between sexes and ages in both chest height and foot-loading. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver, BC, Canada, p. 54.) **Key words: white-tailed deer, moose, elk, bison, snow, morphology**

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_____ **and _____. 1971. Morphological parameters for mammal locomotion in snow. Annual Meeting, American Society of Mammalogists 51.** Measurements were taken of chest heights, foot area, weight, and foot-loading of bison, elk, moose, and white-tailed deer in Elk Island National Park. Replicable measuring procedures are described. Chest heights of the three cervids differed by a fixed interval suggesting resource partitioning with respect to snow. Sex and age differences in morphology may relate to winter mortality. (Annotation by Shank and Bunnell 1982 in *The Effects of Snow on Wildlife: An Annotated Bibliography*, University of BC, Vancouver, BC, Canada, p. 54.) **Key words: bison, elk, moose, white-tailed deer, snow**

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Thompson, I. D. 1980. Effects of weather on productivity and survival of moose in northeastern Ontario. Proceedings of the North American Moose Conference Workshop 16:463-481. Abstract: Weather has been shown to be an important factor affecting calf production and survival, in many parts of the moose range. This effect has not been demonstrated for Ontario. Winter severity, positive energy period, May rainfall and summer rainfall were compared with calves per female in the kill and percent yearlings in the kill by means of multi-variate analysis. Weather, primarily winter severity, was important in affecting production of calves up to the mid-1960s. After 1966, the weather variables tested showed no significant relation to calf production. It is likely that disruption of social structure and *umwelt* through excessive hunting and habitat destruction became more important influences on production, masking any effects of weather. **Key words: moose, precipitation, productivity**

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Toïgo, C., J-M. Gaillard, G. Van Laere, M. Hewison, and N. Morellet. 2006. How does environmental variation influence body mass, body size, and body condition? Doe deer as a case study. Ecography 29(3):301-308. Abstract. We tested the influence of population density and of drought intensity (measured as the Gaussen Index in spring and summer of the year of birth) on winter body mass, hind foot length, and body condition of roe deer fawns. Body mass decreased with increasing density and increased with increasing Gaussen Index in summer, in a similar way for both males and females. Hind foot length of males showed the same response. On the other hand, hind foot length of females decreased with increasing density only after dry summers, hence when environmental conditions were very harsh. Body condition was affected neither by density nor by drought intensity. Our results indicate that body mass and size are much better indicators of phenotypic quality than body condition in roe deer. The sex-specific responses of body size to environmental conditions could correspond to a differential allocation in favor of daughters by heavier than average roe deer mothers. **Key words: roe deer, drought**

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Tveraa, T., P. Fauchald, N. G. Yoccoz, R. A. Ims, R. Aanes, and K. A. Høgda. 2007. What regulate and limit reindeer populations in Norway? Oikos 116:706-715. Abstract: An understanding of how species are affected by top-down and bottom-up processes in food webs, and how these forces interact with climatic conditions is crucial for how ecosystems should be managed. In Norway large carnivores are effectively removed from extensive areas to protect livestock, leaving human harvesting as the only significant top-down force on ungulate populations. We examined the relative role of top-down and bottom-up processes for 58 semi-domesticated reindeer populations in Norway subjected to contrasting climatic regimes over the period 1981-2005. Intensive herding and international agreement have resulted in a situation where some populations are unable to undertake seasonal migration to the interior to escape the unfavorable climatic conditions that rule the coastal region in the winter, a critical season for northern ungulates. We used this natural manipulation to contrast between populations with 'poor' and 'good' winter conditions. For populations with good winter conditions, average body size increased with harvesting, suggesting that some top-down process was necessary to avoid food limitation. Time-series analyses revealed that direct regulation of population size was only evident in populations subjected to intensive harvesting. The lack of direct regulation in populations subjected to low harvesting resulted in high vulnerability to harsh winter weather. The body size and climate vulnerability of populations with poor winter conditions was unaffected of harvesting, but average densities was positively related to overall vegetation productivity as indexed by satellite images (NDVI). Top-down processes appeared to be necessary to dampen the effect of harsh winters in populations with generally good winter conditions. Conversely, populations subjected to generally poor winter conditions appeared to be more influenced by bottom-up processes and buffered climatic perturbations by increasing body size. **Key words: reindeer, morphology**

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Unsworth, J. W., D. F. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho and Montana. Journal of Wildlife Management 63(1):315-326. Abstract: We examined survival rates of mule deer (*Odocoileus hemionus*) fawns (1 Jan-31 May) and adult (≥1 yr old) females (1Jun-31 May) from Colorado, Idaho, and Montana to assess the influence of survival on population dynamics over a broad geographic area. Survival rates were estimated from 1,875 radiocollared fawns and 1,536 radiocollared adult female-years. We found significant year-to-year differences in overwinter survival rates of fawns among states (P<0.001), while annual survival rates of adult females showed less variation across years (P<0.256). Sampling distributions of survival rates by age class were modeled with the beta-binomial distribution (BBD) and not found different among states (ad F:P=0.118; fawns: P=0.856). The mean overwinter survival rate for fawns was 0.444 (SE=0.033), with SD=0.217 (SE=0.019). The mean annual survival rate for adult females was 0.853 (SE=0.011), with SD=0.034 (SE=0.014). All 3 states exhibited differences in body size of fawns at the start of winter across years, and body size was a predictor of overwinter survival (P<0.001). Fawn sex ratios in December at time of capture were not different from 50:50 (P=0.729). However, a sex differential in overwinter survival of fawns was observed (P=0.002), but beta-binomial models of survival distributions were not different between sexes (P=0.458). Frequencies of 3 categories of proximal causes of fawn mortality (predation, winter malnutrition, other) differed among states ($x^2_4 = 41.24$, P<0.001).A deterministic model with a mean winter survival rate of 0.444 for fawns and an annual rate of 0.853 for adult females predicted December fawn:doe ratios would have to be at least 66:100 to maintain population levels. Similarity of mule deer population dynamics across the 3 states suggests similar processes regulate these populations; hence, results from specific study areas are generally more applicable than commonly thought. **Key words: mule deer, morphology, mortality**

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Valdez, R. and L. V. Alamia. 1977. Population decline of an insular population of Armenian wild sheep in Iran. Journal of Wildlife Management 41(4):720-725. From 1970 to 1973, an insular population of Armenian wild sheep (*Ovis orientlis gmelinii*) in an area of 3145 hectares declined from an estimated 3500 to 1000. The dry spring and summer of 1971, the severe winter of 1971-72, and the poor range conditions engendered by heavy overstock were the major factors contributing to the 1971-72 die-off. During that die-off less than 1 percent of the lamb crop survived. Net productivity during 1971, 1982, and 1973 was 14 percent, less than 1 percent, and 15 percent respectively. Under present poor range conditions, the recommended population level is 500 animals. **Key words: wild sheep, drought, forage quality, mortality**

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Van Vuren, D. and M. P. Bray. 1986. Population dynamics of bison in the Henry Mountains, Utah. Journal of Mammalogy 67(3):503-511. Abstract: We assessed structure, survival, productivity, and growth of a *Bison bison* population in southern Utah during 7 years. Consistently female-biased sex ratios resulted from male-biased hunting mortality and possibly from lower survival of young males. Survival, excluding hunting

mortality, was high for all animals and probably was facilitated by a lack of predators and by prolonged parental care of young. Productivity was correlated nonlinearly with precipitation and was lower than in other herds, possibly because of relatively sparse forage. The herd has been increasing exponentially since establishment in the early 1940's, despite annual hunts, low forage production, and possible competition with domestic cattle. Increase has been particularly rapid during an extraordinary series of relatively wet years since the drought of 1977, raising the question of whether the herd has exceeded long-term carrying capacity. **Key words: bison, precipitation, productivity**

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Veeroja, R., V. Tilgar, A. Kirk, and J. Tõnisson. 2008. Climatic effects on life-history traits of moose in Estonia. Oecologia 154(4):703-713. Abstract: Weather variables can influence life-history traits of ungulates. In this study, we assessed the suitability of regional climate indices including the NAO and two measures of local climate—the maximal extent of ice on the Baltic Sea (MIE) and absolute values of its annual deviations from the multi-year mean (VMIE)—to examine how density-independent processes influence moose body size and fecundity. We predicted that both winter severity (large values of MIE) and variability (large values of VMIE) depress moose traits (e.g., severe winters increase energy expenditure because of large snow depth or low temperatures, while the warmer than average winters may impose greater energetic demands on thermoregulation due to wet and windy weather, or may have indirect negative effects on summer foraging conditions). We estimated direct, delayed (lag) and cumulative effects of each climate measure. Both MIE and VMIE negatively affected jawbone length, with the effect size varying between the respective climatic indices and among age classes. In contrast to results obtained using local climatic variables, the NAO index had no significant effect on jawbone length. The probability of multiple ovulation was negatively influenced by direct effects of VMIE and delayed effects of MIE and NAO. We conclude that MIE and VMIE capture different aspects of the local climate and that these indices can be used in parallel as determinants of growth and fecundity of northern ungulates in coastal regions of the Baltic Sea. **Key words: moose, index, fecundity**

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Verme, L. J. 1968. An index of winter weather severity for northern deer. Journal of Wildlife Management 32(3): 566-574. Abstract: The relative severity of winter climate for white-tailed deer (*Odocoileus virginianus*) can be determined by using rather simple and inexpensive equipment to measure the principal stressors, air chill and snow hazard. A rating for air chill is derived with a specially designed chillometer described in this report. Depth of the snow pack and its supporting quality, obtained with a compaction gauge, yield the snow's hazard rating. Respective air chill and snow hazard ratings are summed to compute a weekly severity index. The cumulative total of these values constitutes the seasonal score. Trials within this system in Michigan's Upper Peninsula indicate that it provides a reliable means for judging the physical welfare of yarded deer; hence, their probable mortality rate can be predicted through inspection of collected data as winter progresses. Moderate to heavy deer losses occurred during

winters in which the season's severity index exceeded a value of 100 among the various stations across the peninsula. **Key Words: mortality, white-tailed deer, index**

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_____ **and J. J. Ozoga. 1981. Appraisal of autumn-spring weather severity for northern deer. Wildlife Society Bulletin 9(4):292-295.** Abstract: Verme devised a winter weather severity index that closely correlates with biological parameters indicative of environmental pressure for Michigan whitetails. However, the period of adversity can be prolonged if harsh weather arrives early in autumn and/or extends into late spring. Here we describe a new concept for assessing seasonal weather severity in autumn and spring, using plant phenology instead of climatological data. This methodology enabled us to derive a seasonal numerical index that integrated the various factors affecting vegetation growth; thus, by inference, how weather mediates deer bioenergetics. Moreover, used in conjunction with the winter index, these data provide a means for determining weather severity during an 8-month continuum. Weekly analysis of plant phenology on a few carefully selected plots probably suffices to characterize seasonal weather patterns within a region. Recording the plot coverage percentage for each species present appears to enhance the survey's precision. Plots chosen for this work should be stocked mainly in perennial forbs. Plot analysis by an experienced worker takes just a few minutes; employing the same person annually would ensure comparable data and increase efficiency. **Key words: index, bioenergetics, deer**

365

Visscher, D. R., E. H. Merrill, D. Fortin, and J. L. Frair. 2006. Estimating woody browse availability for ungulates at increasing snow depths. Forest Ecology and Management 222:348-354. Abstract: In northern temperate environments, assessments of ungulate winter range in forested ecosystems commonly focus on measuring availability of browse because the dietary proportion of browse is typically high in winter. In many cases, these efforts ignore reductions in browse availability due to snow burial because this effect is difficult to measure. In this paper, we show how consideration of snow burial can alter the relative availability of browse in 6 forest communities common in the east slopes of the Rocky Mountains of Alberta, Canada. We developed species-specific allometric relationships of stem diameter and woody twig biomass and height for the common shrub species and used these models to predict the decline in the proportion of total biomass/stem available to ungulates relative to stem height. Based on measures of stem densities, we then compared declines in browse availability for all browse species and for preferred browse species with increasing snow depths. Species compositional differences between forest types influenced the decline in browse availability as snow depth increased. Our stem-based approach is more flexible than previous plot-based approaches because it does not assume a distribution in stem heights but uses local information. Adjustments in browse availability are essential in habitat and food selection studies of ungulates where snow accumulates. **Key words: snow, forage quality**

366

Vore, J. M., T. L. Hartman, and A. K. Wood. 2007. Elk habitat selection and winter range vegetation management in northwest Montana. Intermountain Journal of sciences 13(2-3):86-97. Abstract: We determined winter and spring habitat selection of a small (~100) resident elk (*Cervus elaphus*) herd from 1988 to 1998 including 3 years before to 6 years after timber harvest and/or prescribed burns. Sixty-nine elk were fitted with radio transmitters to document elk response to these habitat treatments. The study area was located on Firefighter Mountain along the west shore of Hungry Horse Reservoir in northwestern Montana. Treatments included burning 66 ha of shrubs in eight natural openings and removing coniferous overstory on 251 ha in 48 logging units. We detected no difference pre- to post-treatment in elk selection for the treatment area from within their seasonal home range. Habitat treatments did not influence elk habitat selection. However, snow negatively affected their selection for the treatment area, which suggested forest canopy cover was important to elk in this study area. Thus, opening the forest canopy to increase winter forage production seemingly did not benefit elk. Managers should use caution when managing forests to create forage openings on winter ranges with high snowfall. **Key words: elk, snow, habitat use**

367

Vucetich, J. A., D. W. Smith, and D. R. Stahler. 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. Oikos 111:259-270. Abstract: In the period following wolf (*Canis lupus*) reintroduction to Yellowstone National Park (1995-2004), the northern Yellowstone elk (*Cervus elaphus*) herd declined from ~17,000 to ~ 8,000 elk (8.1%yr^{-1}). The extent to which wolf predation contributed to this decline is not obvious because the influence of other factors (human harvest and lower than average annual rainfall) on elk dynamics has not been quantified. To assess the contribution of wolf predation to this elk decline, we built and assessed models based on elk-related data prior to wolf reintroduction (1961-1995). We then used the best of these models to predict how elk dynamics might have been realized after wolf reintroduction (1995-2004) had wolves never been reintroduced. The best performing model predicted 64% of the variance in growth rate and included elk abundance, harvest rate, annual snowfall, and annual precipitation as predictor variables. The best performing models also suggest that harvest may be super-additive. That is, for every one percent increase in harvest rate, elk population growth rate declines more than one percent. Harvest rate also accounted for ~47% of the observed variation in elk growth rate. According to the best-performing model, which accounts for harvest rate and climate, the elk population would have been expected to decline by 7.9% per year, on average, between 1995 and 2004. Within the limits of uncertainty, which are not trivial, climate and harvest rate are justified explanations for most of the observed elk decline. To the extent that this is true, we suggest that between 1995 and 2004 wolf predation was primarily compensatory. **Key words: elk, predation, model**

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Wallace, L. L., M. G. Turner, W. H. Romme, and Y. Wu. n.d. Bison and fire: landscape analysis of ungulate response to Yellowstone's fires. International Bison Conference, July 27, 1993, LaCrosse, Wisconsin. Conf-9307151-1, USDOE,

Washington, D.C. Abstract: A simulation model of bison survival under different scenarios of winter severity, fire size, fire pattern and population size was run. Previous work had shown the model to be realistic. The overriding factor influencing bison winter survival in the model was winter severity. This factor had significant interactions with fire size and population size as well, further reducing survival in all cases. Increasing fire size reduced survival the first year after a simulated fire, but increased survival two years after the fire. This was due to enhanced forage production in burned areas the second year. A threshold effect on survival was noted at fire sizes greater than 60% of the simulated landscape, a number which is critical in disturbance propagation in landscapes. There was no biologically important effect of fire pattern (random vs. clumped) on survival. **Key words: bison, fire, mortality, model**

369

Wallmo, O. C. and R. B. Gill. 1971. Snow, winter distribution, and population dynamics of mule deer in the central Rocky Mountains. Pages 1-15 *in* A. O. Haugen, editor. Proceedings of the Snow and Ice in Relation to Wildlife and Recreation Symposium, Iowa State University, 11-12 February, Ames, Iowa. Abstract: The relationship between snow and mule deer distribution and population dynamics is discussed. On selected study areas in Middle Park, Colorado, we observed that winter snow accumulations determined the amount of potential winter range available to deer each year. During heavy snow winters availability of winter range was so reduced that carrying capacity of winter ranges was negligible, and this was followed by subsequent declines in the deer population. Winters of light snow accumulations were followed by population increases. Following light snow winters mortality was low and productivity was high, while heavy snow winters resulted in high mortality rates and low productivity rates. **Key words: snow, mortality, fecundity**

370

_____, A. W. Jackson, T. L. Hailey, and R. L. Carlisle. 1962. Influence of rain on the count of deer pellet groups. Journal of Wildlife Management 26(1):50-55. Summary: Data from two study areas in the semiarid mountains of western Texas reveal that rainfall is a major cause of the disappearance of deer pellet groups, thereby influencing the effectiveness of the pellet-group count method for estimating population densities. The only reasonable expedient seems to be that of making pellet-group counts only during dry periods. **Key words: deer, precipitation, technique, census**

371

Wang, G., N. T. Hobbs, F. J. Singer, D. S. Ojima, and B. C. Lubow. 2002. Impacts of climate changes on elk population dynamics in Rocky Mountain National Park, Colorado, USA. Climatic Change 54: 205-223. Abstract: Changing climate may impact wildlife populations in national parks and conservation areas. We used logistic and non-linear matrix population models and 35 years of historic weather and population data to investigate the effects of climate on the population dynamics of elk in Rocky Mountain National Park (RMNP), Colorado, U.S.A. We then used climate scenarios derived from Hadley and Canadian Climate Center (CCC) global climate models to project the potential impacts of future climate on the elk population. All models revealed density-

dependent effects of population size on growth rates. The best approximating logistic population model suggested that high levels of summer precipitation accelerated elk population growth, but higher summer minimum temperatures slowed growth. The best approximating non-linear matrix model indicated that high mean winter minimum temperatures enhances recruitment of juveniles, while high summer precipitation enhanced the survival of calves. Warmer winters and wetter summers predicted by the Hadley Model could increase the equilibrium population size of elk by about 100%. Warmer winters and drier summers predicted by the CCC Model could raise the equilibrium population size of elk by about 50%. Managers of national park have relied on effects of weather, particularly severe winters, to regulate populations of native ungulates and prevent harmful effects of overabundance. Our results suggest that these regulating effects of severe winter weather may weaken if climate changes occur as those that are widely predicted in most climate change scenarios. **Key words: elk, recruitment, temperature, precipitation**

372

Ward, R. L. and C. L. Marcum. 2005. Lichen litterfall consumption by wintering deer and elk in western Montana. Journal of Wildlife Management 69(3):1081-1089. Abstract: We studied arboreal lichen production and availability for Rocky Mountain elk (*Cervus elaphus nelsoni*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*) during winter in western Montana, USA. In May and June of 1997 and 1998, we collected lichen litterfall inside and outside exclosures to assess deer and elk use of lichens and recorded associated tree stand characteristics. *Bruproa* spp. and *Nodobryoria* spp. composed >99% of the lichen litterfall. Lichen litterfall use by deer and elk on 2-yr sites averaged 7.91 kg/ha for the severe winter of 1996-1997, and 6.02 kg/ha for the milder winter of 1997-1998. The greater use of lichens in winter 1996-1997 was probably due to increased ungulate densities in forested habitats during a severe winter. A strong linear relationship between lichen availability and lichens consumed suggested that lichen use was driven by availability rather than opportunistic foraging and that ungulates may have selected habitat partly because of lichen availability. Tree stand variables were partially correlated with lichen availability and consumption by ungulates but were different between winters, indicating that variables in addition to those we measured contributed to availability and consumption. **Key words: elk, white-tailed deer, snow**

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Watson, A. 1971. Climate and antler-shedding and performance of red deer in north-east Scotland. Journal of Applied Ecology 8(1):53-67. Abstract: Watson tested the null hypothesis that there was no difference in Scottish red deer antler shedding between years and examined antler-shedding in relation to the deer's population processes. Data from 17 years compare antler-shedding with climate and with molt, condition, reproductive performance and mortality. Results show that the timing of antler-shedding is a useful portent of these subsequent aspects of deer performance and may be useful for practical deer management because the method is so simple. (1) On any one area, the timing of antler-shedding in red deer was earlier (P<0.001) after fairly snow-free winters than after snowy winters. On different areas in the same year, stags at high altitudes were later (P<0.001) in shedding antlers than stags at low altitudes.

However, the rate at which antlers were shed did not vary significantly between snowy and fairly snow-free years, or between high and low altitudes. (2) Stags in good condition were early in shedding old antlers and growing new ones, in molting their grey-brown winter coats, and in growing their new red summer coats. Of the many stags that were found dead from March to early May, none had shed its antlers, and all were in poor condition. (3) At one place, stags which ate artificial food (human refuse) daily in winter were tamest toward man, were the most dominant individuals, and were the earliest to shed antlers. (4) After cold snowy winters many deer died and the percentage of the previous year's calves was low among groups of hinds and calves counted in May, and the percentage of current year's calves in these groups was low in September (highly significant correlations with the duration of snow-lie the previous winter). Thus, the timing of antler-shedding in early spring is a useful portent of condition, mortality, and breeding performance of the stock subsequently in late spring and summer. **Key words: red deer, antler, index**

374

Wegge, P. 1975. Reproduction and early calf mortality in Norwegian red deer. Journal of Wildlife Management 39(1):92-100. Abstract: This paper reports the results of a comparative study on reproduction of an island population (Hitra) and an adjacent mainland population (Aure) of red deer (*Cervus elaphus*) in Norway. In both populations, the potential reproductive rate of hinds 2.5 years old and older was over 90 percent. Nearly 50 percent of Aure yearlings ovulated and conceived, but yearlings on the Island did not conceive. Later sexual maturation of Hitra deer seemed related to smaller body size, but not necessarily to slower animal growth rate. The difference may have a genetic basis. If the delay in puberty in Hitra deer is due to environmental differences, quality of spring and summer food appears the most important factor. Autumn recruitments of calves varied significantly within each area in two consecutive years. An estimated high calf loss of 41 percent in Aure during 1971 may have resulted from nutritional failure of pregnant hinds in late winter and spring imposed by adverse weather conditions. Retardation of skeletal growth in immature animals was used as indirect evidence for this view. **Key words: red deer, nutrition, fecundity**

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Wehausen, J. D. 2005. Nutrient predictability, birthing seasons, and lamb recruitment for desert bighorn sheep. Pages 37-50 *in* J. Goerrissen and J. M. André, eds. Sweeney Granite Mountains Desert Research Center 1978-2003: A quarter century of research and teaching. University of California Natural Reserve Program, Riverside, USA. Wehausen studied the question of nutrient predictability using long-term data on diet quality patterns of bighorn sheep from three populations in the eastern Mojave Desert of California. He analyzed patterns of nutrient availability relative to timing of birthing and the survivorship of lambs. Diet quality of sheep was tracked via percent nitrogen in feces (FN). He found there is a predictable timing of the winter-spring growing season that determines diet quality for sheep. In contrast, forage growth from summer rainfall yields minimal nutritional gains for these sheep. Rainfall in October and February has different effects on vegetation growth. Fall rainfall is important for initiating the growth of cold-tolerant species; February rainfall is important for continuance of growth of those cold-tolerant species that might have been initiated

earlier, but also is important for growth of cold-intolerant perennial species during spring. The forage species initiated by fall rains provide the first new green growth eaten by sheep. Early precipitation determines the diet quality level at that first sampling. Summer rains clearly produce much less nutrient availability for sheep than cold season rains; temperature is fundamental. Cold season precipitation mostly occurs as soaking rains that persist for long periods as soil moisture because of subsequent cool temperatures. In contrast, much of summer rainfall runs out of the mountain ranges as flash floods to habitats not used by sheep. What moisture makes it into the soil in sheep habitat evaporates rapidly due to hot temperatures. Relatively few species respond to hot season rains compared with cool season rains. There is a high temporal predictability of diet quality for sheep. Birthing seasons of desert bighorn typically show a clear winter-spring peak that is aligned well with diet quality patterns. The survival of lambs to summer is strongly influenced by the amount of body growth they put on in spring.

October-April rainfall probably has a small effect on the timing of the birthing season from the following year through its effect on subsequent body condition of females and the effect of body condition on timing of ovulation. In contrast, the amount of rainfall during October-April has a major effect on the survivorship of lambs to summer. That relationship is more complex than expected, with strong gains in survivorship up to about 23 cm of rainfall, but decreasing survivorship associated with rainfall beyond that amount.

While diet quality of sheep benefits from increasing growing season precipitation, so do insect populations. It is possible that the declining lamb recruitment in the study is also due to a disease that is adequately spread among sheep by arthropods only during very wet years. **Key words: wild sheep, mortality, disease, precipitation, diet, fecundity**

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_____. 1992. The role of precipitation and temperature in the winter range diet quality of mountain bighorn sheep of the Mount Baxter herd, Sierra Nevada. Proceedings of the Biennial Symposium, Northern Wild Sheep and Goat Council 8:279-292. Abstract: The study of population ecology of wild ungulates often has emphasized the role of nutrition relative to demography, notably reproduction and survival. Consequently, diet quality is an important consideration in modeling such populations. An assessment of the principle environmental variables driving winter range diet quality of mountain sheep from the Mount Baxter population in the Sierra Nevada was made using 14 years of fecal crude protein data. Fecal crude protein, a measure of diet digestibility, should reflect the availability of growing plant tissues, which in turn should reflect the role of temperature and precipitation. The amount of winter precipitation proved to be a relatively unimportant influence, while the timing of the first major storm that initiated plant growth was very important. Second in importance was temperature. These results are discussed in the context of application to demographic models. **Key words: wild sheep, temperature, precipitation, nutrition**

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_____, V. C. Bleich, B. Blong, and T. L. Russi. 1987. Recruitment dynamics in a southern California mountain sheep population. Journal of Wildlife Management 51(1):86-98. Abstract: Lamb:ewe ratio data spanning the years 1953-82 for mountain

sheep (*Ovis canadensis*) in the Santa Rosa Mountains of southern California were analyzed by multiple regression to investigate hypothesized controlling factors. Precipitation during November, January, and February as independent variables each showed a significant positive influence on recruitment rate, in accord with expectations for this desert environment. Between 1962 and 1976, an unidentified 4th factor (probably rising population density) caused a slow decline in recruitment ratio. This ratio plummeted in 1977 and averaged about 25% of the ratio predicted from precipitation alone for 1977-82, a period coincident with a suspected disease epizootic. A similar period of depressed lamb recruitment was found for the 1953-61 period, suggesting the possibility of a recurrent phenomenon. Data needs and various hypotheses concerning factors potentially underlying the observed and future population dynamics are discussed. **Key words: wild sheep, precipitation, population dynamics**

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Weladji, R. B., Ø. Holand, G. Steinheim, J. E. Colman, H. Gjostein, and A. Kosmo. 2005. Sexual dimorphism and intercorhort variation in reindeer calf antler length is associated with density and weather. Oecologia 145:549-555. Abstract: We analysed intercohort variability of live weight and antler length of 5,123 reindeer calves. We further assessed the influence of climate and density on the interannual variation in antler length, and discussed sex-specific resource allocation and response to climate variability. Antler length varied significantly among years and between sexes, with interaction between year and sex. Body weight and antler length were highly positively correlated, showed similar intercohort variability, and had a strong allometrical link, suggesting that antler length could be an equally reliable measure of calf condition as live weight. We found a relative measure of antler length (i.e. antler length corrected for the allometric effect of body mass) to be positively influenced by increasing density and May-June precipitation, and also decreasing May-June temperature. We attributed the effect of early summer weather to its influence on forage availability and quality as well as the level of parasitic insect harassment. Gender difference in both the allometric exponents and the interannual variability suggest that young males and females may have different tactics for relative resource allocation towards growth of antlers as compared to body mass. Because antlers are costly to produce, they may be an honest signal of individual quality for both sexes. However, we found gender-specific allometry, as female calves more than males appear to prioritize their antler growth over body mass, especially when resources are limited. Thus, our results suggest that environmental variation may influence the extent of sexual dimorphism in antler length. **Key words: caribou, antler, density, precipitation, temperature**

379

_____and Ø. Holand. 2003. Global climate change and reindeer: effects of winter weather on the autumn weight and growth of calves. Oecologia 136:317-323. Abstract: Reindeer/caribou (*Rangifer tarandus*), which constitute a biological resource of vital importance for the physical and cultural survival of Arctic residents, and inhabit extremely seasonal environments, have received little attention in the global change debate. We investigated how body weight and growth rate of reindeer calves were affected by large-scale climatic variability [measured by the North Atlantic Oscillation (NAO) winter index] and density in one population in central Norway. Body weights of

calves in summer and early winter, as well as their growth rate (summer to early winter), were significantly influenced by density and the NAO index when cohorts were *in utero*. Males were heavier and had higher absolute growth than females, but there was no evidence that preweaning condition of male and female calves were influenced differently by the NAO winter index. Increasing NAO index had a negative effect on calves' body weight and growth rate. Increasing density significantly reduced body weight and growth rate of calves, and accentuated the effect of the NAO winter index. Winters with a higher NAO index are thus severe for reindeer calves in this area and their effects are associated with nutritional stress experienced by the dams during pregnancy or immediately after calving. Moreover, increased density may enhance intra-specific competition and limits food available at the individual level within cohorts. We conclude that if the current pattern of global warming continues, with greater change occurring in northern latitudes and during winter as is predicted, reduced body weight of reindeer calves may be a consequence in areas where winters with a high NAO index are severe. This will likely have an effect on the livelihood of many northern indigenous peoples, both economically and culturally. **Key words: caribou, NAO, morphology**

380

_____, Ø. Holand, and T. Almøy. 2003. Use of climatic data to assess the effect of insect harassment on the autumn weight of reindeer (*Rangifer tarandus*) calves. Journal of Zoology London 260:79-85. Abstract: Considerable behavioral evidence supports harassment by insects as the most important causal link between warm summer temperatures and low body condition of reindeer *Rangifer tarandus*, and that insect activity is influenced by weather condition. However, much less is known about the effect of insect harassment on individual performance, measured as reduced weight gain during summer, and the related consequences on both the reindeer pastoral economy and reindeer as a biological resource. Using climatic data, this paper develops a simple index for the analysis of insect harassment that takes into consideration weather variables known to significantly affect insect activity and/or the level of insect harassment. The insect harassment index, which is based on mid-day ambient temperature $\geq$ 13°C, wind speed < 6 m/s and cloud cover < 40%, is further used to test the hypothesis that insect harassment has a negative effect on reindeer performance during summer in three Norwegian populations. Results show that harassment by insects negatively affects the autumn weight of reindeer calves, most probably through reduced grazing time and increased energy expenditure, but also indirectly by negatively influencing milk production of the dam. Moreover, female calves were more vulnerable to insect harassment than males. Insect harassment may have consequences on future reproductive performance, calving time, calf birth weight and hence neonatal mortality, and thus affect reindeer productivity. The present index is easy to estimate and may be used to quantify and compare harassment levels on various reindeer summer grazing areas for management purposes. Our results also suggest that the expected temperature increase in the course of global warming may increase the insect-related stress on reindeer. **Key words: index, temperature, insects, productivity**

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_____, Ø. Holand, N. G. Yoccoz, and D. Lenvik. 2003. Maternal age and offspring sex ratio variation in reindeer (*Rangifer tarandus*). Annals Zoologici Fennici

40:357-363. Abstract: Different evolutionary hypotheses have been proposed to explain variation in offspring sex ratios among mammalian populations. The Trivers and Willard and local resource competition hypotheses, which are based on adaptive modification by maternal investment, are two opposing hypotheses commonly used for ungulates, but empirical patterns often do not fit either hypotheses' expectations. We investigated sex ratio variation in 1658 reindeer (*Rangifer tarandus*) calves in relation to their mothers' mass and age, while accounting for potential density-independent factors such as climate. The most parsimonious model included only the effect of maternal age, the proportion of males increasing with increasing maternal age. Similar models in terms of parsimony included (in addition to maternal age) the winter temperature or the North Atlantic Oscillation (NAO) index when the mothers were *in utero*, indicating that climatic conditions experienced by mothers in their year of birth, have the potential to influence variation in a cohort's offspring sex ratio. Thus, a combination of both density-dependent and density-independent factors may influence sex ratio variation in reindeer and perhaps in other ungulates. We suggest that, if an adaptive maternal strategy is present, it may be induced and/or inhibited by, or interact with, other factors such as climate. **Key words: caribou, sex ratio, NAO**

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_____, D. R. Klein, Ø. Holand, and A. Mysterud. 2002. Comparative response of *Rangifer tarandus* and other northern ungulates to climatic variability. Rangifer 22(1): 29-46. Abstract: To understand the factors influencing life history traits and population dynamics, attention is increasingly being given to the importance of environmental stochasticity. In this paper, we review and discuss aspects of current knowledge concerning the effect of climatic variation (local and global) on population parameters of northern ungulates, with special emphasis on reindeer/caribou (*Rangifer tarandus*). We also restrict ourselves to indirect effects on climate through both forage availability and quality, and insect activity. Various authors have used different weather variables, with sometimes opposite trends in resulting life history traits of ungulates, and few studies show consistent effects to the same climatic variables. There is thus little consensus about which weather variables play the most significant role influencing ungulate population parameters. This may be because the effects of weather on ungulate population dynamics and life history traits are scale dependent and it is difficult to isolate climatic effects from density dependent factors. This confirms the complexity of the relationship between environment and ecosystem. We point out limits of comparability between systems and the difficulty of generalizing about the effect of climate change broadly across northern systems, across species and even within species. Furthermore, insect harassment appears to be a key climate-related factor for the ecology of reindeer/caribou that has been overlooked in the literature of climatic effects on large herbivores. In light of this, there is a need for further studies of long time series in assessing effects of climate variability on reindeer/caribou. **Key words: caribou, insects, moose, red deer, sex ratio**

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West, D. R. 1970. Effects of prolonged deep snow and cold winters on pronghorn mortality and reproduction in South Dakota, Proceedings of the Antelope States Workshop 4:41-49. Summary: The 1948-49 data strongly indicate winter movement out

of deep snow areas to more protected or windswept areas. Shorter moves were noted in early 1965. Information on time lapse or rate of return to former home range is lacking. It may be pertinent to note that in early 1949 movement was unhindered by cross fencing as it is today.

Adult mortality was observed in the winters of 1948-49, 1964-65, and 1968-69. Starvation or malnutrition was the obvious cause of death in observed animals. No large scale die-offs were observed due to winter weather. (An exception may exist in the 1964-66 period when this writer misplaced 2,200 head of antelope and has not gotten the books back in order.)

Reduced productivity as expressed in doe:kid ratios may have occurred in Meade County in 1949. It definitely was noted in 1965 in Harding, Butte, Meade, Perkins, and Corson Counties, and in 1969 in Harding, Perkins, and Corson Counties.

Cold temperatures without deep snow cover to reduce available browse had no apparent effect on the spring population or doe:kid ratio in Meade County in 1969.

High productivity shown by the 1950 and 1966 doe:kid ratios indicates antelope does are able to regain body condition and successfully conceive following a severe winter.

Key words: antelope, snow, temperature, mortality, productivity

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White, P. J., J. E. Bruggeman, and R. A. Garrott. 2007. Irruptive population dynamics in Yellowstone pronghorn. Ecological Applications 17(6):1598-1606.

Abstract: Irruptive population dynamics appear to be widespread in large herbivore populations, but there are few empirical examples from long term series with small measurement error and minimal harvests. We analyzed an 89-year time series of counts and known removals for pronghorn (*Antilocapra americana*) in Yellowstone National Park of the western United States during 1918-2006 using a suite of density-dependent, density-independent, and irruptive models to determine if the population exhibited irruptive dynamics. Information-theoretic model comparison techniques strongly supported irruptive population dynamics (Leopold model) and density dependence during 1918-1946, with the growth rate slowing after counts exceeded 600 animals. Concerns about sagebrush (*Artemisia* spp.) degradation led to removals of >1100 pronghorn during 1947-1966, and counts decreased from approximately 700 to 150. The best models for this period (Gompertz, Ricker) suggested that culls replaced intrinsic density-dependent mechanisms. Contrary to expectations, the population did not exhibit enhanced demographic vigor soon after the termination of the harvest program, with counts remaining between 100 and 190 animals during 1967-1981. However, the population irrupted (Caughley model with a one-year lag) to a peak abundance of approximately 600 pronghorn during 1982-1991, with a slowing in growth rate as counts exceeded 500. Numbers crashed to 235 pronghorn during 1992-1995, perhaps because important food resources (e.g., sagebrush) on the winter range were severely diminished by high densities of browsing elk, mule deer, and pronghorn. Pronghorn numbers remained relatively constant during 1996-2006, at a level (196-235) lower than peak abundance, but higher than numbers following the release from culling. The dynamics of this population supported the paradigm that irruption is a fundamental pattern of growth in many populations of large herbivores with high fecundity and delayed density-dependent effects on recruitment when forage and weather conditions become favorable after range expansion or release from harvesting. Incorporating known removals into

population models that can describe a wide range of dynamics can greatly improve our interpretation of observed dynamics in intensively managed populations. **Key words: antelope, range quality, fecundity**

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Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parish 1984. Food intake and foraging energetics of elk and mule deer. Journal of Wildlife Management 48(4):1285-1301. Abstract: The energetic cost of grazing was measured using indirect calorimetry with a tracheotomized elk (*Cervus elaphus nelsoni*). The cost of eating herbaceous forage averaged 0.32 kcal/kg body weight/hour, an energetic increment of 26% over standing costs. Forage intake was quantified using esophageal fistulated elk and mule deer (*Odocoileus hemionus hemionus*). Dry matter consumption rate and mean bite size increased curvilinearly as functions of forage biomass for both species. Asymptotic grass intake rates were 2.22 and 14.04 g dry matter/minute for deer and elk, respectively. Consumption rate and bite size were greater in shrub-forb communities than on grass pastures of comparable biomass. Biting rate ranged from about 15 to 60 bits/minute and was inversely related to bite size. Rate of travel during foraging decreased exponentially with increasing forage availability. A computer model was constructed to evaluate the interaction of time and energy constraints on foraging ungulates. The effects of variation in forage quality, forage abundance, and snow cover on the ability of animals to meet daily energy requirements are discussed. **Key words: elk, mule deer, snow, bioenergetics, nutrition, model**

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Wilmers, C. C., E. Post, R. O. Peterson, and J. A. Vucetich. 2006. Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. Ecology Letters 9:383-389. Abstract: Human-introduced disease and climatic change are increasingly perturbing natural ecosystems worldwide, but scientists know very little about how they interact to affect ecological dynamics. An outbreak of canine parvovirus (CPV) in the wolf population on Isle Royale allowed us to test the transient effects of an introduced pathogen and global climatic variation on the dynamics of a three-level food chain. Following the introduction of CPV, wolf numbers plummeted, precipitating a switch from top-down to bottom-up regulation of the moose population; consequently, the influence of climate on moose population growth rate doubled. This demonstrates that synergistic interactions between pathogens and climate can lead to shifts in trophic control, and suggests that predators in this system may play an important role in dampening the effects of climate change on the dynamics of their prey. **Key words: moose, disease, mortality**

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Wilson, R. R. and P. R. Krausman. 2008. Possibility of heat-related mortality in desert ungulates. Journal of Arizona-Nevada Academy of Science 40(1):12-15. Abstract: Studies on mortality of young ungulates in arid environments usually restrict the possible causes of death to predation, starvation, or disease. However, hyperthermia as a cause of death in wild animals living in arid environments is rarely discussed or considered and might be a source of mortality in juveniles. During a two-week period

after 11 July 2005, four Sonoran pronghorn (*Antilocapra americana sonoriensis*) fawns (4-5 months old) died of unknown causes in a 130-ha enclosure in southern Arizona. Predation did not appear to be the cause of death. Likewise, starvation does not appear to be the cause of death because fawns did not exhibit observable signs of malnutrition prior to the period of their death. Disease also appears to be unlikely because the timing of occurrence of the vector for the two main diseases known to occur in the population (i.e., blue tongue and epizootic hemorrhagic disease [EHD]) does not coincide with the fawn deaths (although this does not rule out other potential disease). Hyperthermia might have been the cause of death of the four fawns because the three hottest days of the year (44.1, 44.1, and 43.6°C) occurred during the period the fawns died. While our evidence for hyperthermia as the cause of death is speculative, biologists should consider the possibility that young desert-dwelling ungulates may be susceptible to hyperthermia during the hottest period of the year and that it might be a source of fawn mortality that cannot be managed. **Key words: antelope, temperature, hyperthermia, solar radiation, mortality**

388

Wishart, W. 2006. Bighorns and little horns revisited. Proceedings of Northern Wild Sheep and Goat Council 15:28-32. Abstract: During the 1960s a series of horn measurements of bighorn rams (*Ovis canadensis*) from the eastern slopes of Alberta was recorded. The horn base circumferences of rams from the Chinook belt south of the Bow River were significantly larger than ram horns to the north. A subsequent series of horn base measurements up to forty years later had the same results. However, there were some notable exceptions in central and northern Alberta. Ram horn bases increased significantly following a controlled ewe removal program in central Alberta on Ram Mountain and decreased to former levels after cessation of ewe removals. Ram horns at northern coal mine reclamation sites had larger horn bases than ram horn measurements prior to reclamation. **Key words: wild sheep, horn, nutrition, temperature, wind**

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_____. 1969. Bighorns and little horns. Alberta: Lands-Forests-Parks-Wildlife 12(3):5-10. Abstract: It has long been noted that bighorn rams in the south of Alberta have significantly larger horns than rams in the north, and the change is pronounced at the Bow River west of Calgary. Wishart found that the horns of southern Alberta rams are more massive and grow more rapidly than those of northern Alberta, and in general are larger than sheep of the north. Around the Bow River there is a black soil zone, the most fertile in Alberta. The dominant grass in this area is rough fescue (*Festuca scabrella*). Also, there are frequent Chinooks south of the Bow River while the north has longer periods between Chinooks. Chinooks remove snow accumulation allowing animals easier access to forage. In summary, southern Alberta exhibits a combination of climate, soil and vegetation that produces large sheep and rams with very large horns. **Key words: wild sheep, horn, wind, nutrition, temperature**

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Wood, A. K. 1988. Use of shelter by mule deer during winter. Prairie Naturalist 20(1):15-22. Abstract: A study was conducted during winter months of 1984 to evaluate the use of topographic shelter by mule deer (*Odocoileus hemionus*) in a prairie habitat. Deer selected bedding sites that were warmer and less windy than randomly selected adjacent sites. Feeding deer selected sites that were only less windy. Wind velocity seemed to be the most important factor influencing selection of both bedding and feeding sites. Deer used topographic features to minimize effects of windchill. They also seemed to minimize net energy loss by bedding rather than feeding as environmental conditions worsened. Implications of shelter use to over-winter energy budgets of deer are discussed. **Key words: mule deer, wind, temperature, behavior**

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Woodard, T. N., R. J. Gutiérrez, and W. H. Rutherford. 1974. Bighorn lamb production, survival and mortality in south-central Colorado. Journal of Wildlife Management 38(4):771-774. Abstract: A bighorn sheep (*Ovis canadensis*) herd was observed in the Sangre de Cristo Mountains of Colorado during the spring, summer, and fall of 1969 and the summer and fall of 1970. June ewe-lamb ratios were 100:83 in 1969 and 100:72 in 1970. High late summer lamb mortality occurred during both years, with the ewe-lamb ratio being 100:17 by September 1969, and 100:22 by September 1970. Lamb mortality resulting from predation or accidents was not found to be a factor. Disease, possibly enhanced by inclement weather, was believed to be a significant factor in lamb mortality. Two lambs were collected in 1970, and both displayed a verminous pneumonia of lungworm (*Protostrongylus stilesi*) origin and a broncho-pneumonia of probable bacterial origin. **Key words: wild sheep, productivity, mortality, disease, precipitation, temperature**

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Woodward, T., C. Hibler, and B. Rutherford. 1972. Bighorn lamb mortality investigations in Colorado. Pages 44-48 *in* E. G. Scheffler, chairman. Transactions of the 1972 Northern Wild Sheep Council. Compiled by the Alberta Fish and Wildlife Division, Department of Lands and Forests. Notes: Lamb mortality in the Sangre de Cristo mountain range of Colorado in the 1960s was studied. The peak in lamb losses during two summers appeared to coincide with a period of cold, wet weather, more or less typical of the Colorado Rockies during August. Critical analysis of the combination of circumstances and conditions encountered by these bighorns seemed to support the conclusion that high lamb mortality was the result of respiratory disease caused by lung parasitism, enhanced by inclement weather at critical periods, with possible nutritional deficiencies or imbalances contributing. **Key words: wild sheep, mortality, disease, precipitation, temperature**

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Yom-Tov, Y. and E. Geffen. 2006. Geographic variation in body size: the effects of ambient temperature and precipitation. Oecologia 148:213-218. Abstract: Latitudinal trends in body size have been explained as a response to temperature- or water-related factors, which are predictors of primary production. We used the first principal

component calculated from three body parameters (weight, body length and the greatest length of the skull) of a sample of mammals from Israel and Sinai to determine those species that vary in size geographically, and whether such variation is related to annual rainfall, average minimum January temperature and average maximum August temperature. We used a conservative approach to discern the effects of precipitation and temperature by applying sequential regression. Variable priorities were assigned according to their bivariate correlation with body size, except for rainfall and its interactions that entered into the model last. Eleven species (*Acomys cahirinus, Apodemus mystacinus, Canis lupus, Crocidura suaveolens, Gerbillus dasyurus, Hyaena hyaena, Lepus capensis, Meles meles, Meriones tristrami, Rousettus aegyptius* and *Vulpes vulpes*) of the 17 species examined varied in size geographically. In five of them, rainfall was positively related to body size, while in one species it was negatively related to it. Contrary to the prediction of Bergmann's rule, mean minimum January temperature was positively related to body size in five species and negatively related to body size in two species (*C. suaveolens* and *G. dasyurus*). As predicted by Bergmann's rule, maximum June temperature was negatively related to body size in three species, and positively so in one (*L. capensis*). Primary production, particularly in desert and semi-desert areas, is determined mainly by precipitation. The above results indicate that, in our sample, primary production has an important effect on body size of several species of mammals. This is evident from the considerable proportion of the variability in body size explained by rain. However, low ambient temperatures may slow down and even inhibit photosynthesis. Hence, the observed positive relationships between average minimum January temperature and body size in four of the six species influenced by rain further support this conclusion. **Key words: precipitation, temperature, morphology**

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Zagata, M. D. and A. O. Haugen. 1974. Influence of light and weather on observability of Iowa deer. Journal of Wildlife Management 38(2):220-228. Abstract: The individual and combined effects of light intensity and various weather phenomena on numbers of white-tailed deer (*Odocoileus virginianus*) seen per observation were correlated by multiple regression analysis using the model with deer sighted (adults, juveniles, antlerless, antlered, and unknown) versus sunset or sunrise time, time of sighting, location, lunar phase, minimum daily temperature, maximum daily temperature, wind direction, wind velocity, nebulosity, type of precipitation, amount of precipitation, type of ground cover, and amount of snow on the ground. Observations were made from a blind during crepuscular periods from September through May. A significant relationship ($P<0.05$) to the number of deer sighted per sighting existed with the effects of: time of sunrise, time of sunset, maximum temperature, minimum temperature, wind direction, wind velocity, and ground cover. These effects were not the same for all age and sex classes, and in some instances, different effects were observed for the dawn and dusk periods. **Key words: white-tailed deer, temperature, wind, snow, census**

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Zannèse, A., A. Baïsse, J.-M. Gaillard, A. J. M. Hewison, K. Saint-Hilaire, C. Toïgo, G. Van Laere, and N. Morellet. 2006. Hind foot length: an indicator for monitoring roe deer populations at a landscape scale. Wildlife Society Bulletin 34(2):351-358. Abstract: Wildlife managers frequently use estimates of population densities to guide

ungulate management. Because it is nearly impossible to obtain accurate counts, these estimates are based in indices. Thus, managers continue to seek new index methods that could help them better monitor and manage ungulate populations. In this paper we examine the usefulness of hind foot length as an ecological indicator of density dependence for monitoring roe deer (*Capreolus capreolus*) populations. We used the hind feet of all roe deer shot over an entire province for 13 years that were collected by wildlife managers from the Tarn Hunter Federation (France) to conduct this research. Information on the sex, date and shooting locality were recorded by hunters, and animal age was determined by wildlife managers. We divided the province into 3 biogeographical regions and investigated the relationship between hind foot length of roe deer fawns, spring and summer climate (temperature and precipitation), and an index of deer density (number of shot roe deer per square kilometer) by region using linear models. Hind foot length differed between sexes and between regions. In 2 out of 3 regions, we observed a negative relationship between hind foot length and our index of roe deer density. Further, hind foot length was lower when springs (but not summers) were cold or wet. We interpreted these trends in relation to changes in population density and habitat structure. We concluded that hind foot length is a useful indicator for assessing the density-dependent relationship between roe deer populations and their environment and for monitoring population trends. **Key words: roe deer, index, temperature, precipitation, monitoring**

Ungulate Taxa

Common Name	***Scientific Name***
Arabian Oryx	*Oryx leucoryx*
Argali	*Ovis ammon ammon*
Armenian Wild Sheep	*Ovis orientalis gmelini*
Asiatic Ass	*Equus hemionus*
Bison	*Bison bison*
Black-tailed deer	*Odocoileus heminous columbianus*
Blue wildebeest	*Connochaetes taurinus*
Caribou	*Rangifer tarandus*
Chamois	*Rupicapra rupicapra*
Dall's Sheep	*Ovis dalli dalli*
Desert Bighorn	*Ovis canadensis nelsoni*
Eland	*Tragelaphus (Taurotragus) oryx*
Elk	*Cervus elaphus*
European Bison	*Bison bonasus*
European Roe Deer	*Capreolus capreolus*
Gazelle, Mongolian	*Procapra gutturosa*
Gemsbok	*Oryx gazella*
Hartebeest, Red	*Alcelaphus buscelaphus caama*
Ibex	*Capra ibex*
Impala	*Aepyceros melampus*
Isard	*Rupicapra rupicapra*
Kudu	*Tragelaphus strepsiceros*
Moose	*Alces alces*
Mouflon	*Ovis ammon musimon*
Mountain Goat	*Oreamnos americanus*
Mule Deer	*Odocoileus hemionus*
Muskoxen	*Ovibos moschatus*
Pronghorn	*Antilocapra Americana*
Red Deer	*Cervus elaphus*
Rocky Mountain Bighorn	*Ovis canadensis canadensis*
Saiga Antelope	*Saiga tatarica*
Serow	*Capricornis crispus*
Sika Deer	*Cervus nippon*
Sitka Deer	*Odocoileus hemionus sitkensis*
Soay Sheep	*Ovis aries*
Stone's Sheep	*Ovis dalli stonei*
Tibetan Antelope	*Patholops hodgsoni*
Tsessebe	*Damaliscus lunatus*
White-tailed Deer	*Odocoileus virginianus*
Wildebeest	*Connochaetes taurinus*

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