Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*)

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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: bighorn sheep, density-dependence, weather, population dynamics, juvenile survival

INTRODUCTION

In ungulates, juvenile survival is typically lower and more variable than adult survival, and is generally thought to be more sensitive to changes in weather and resource availability (Sinclair, 1977; Fowler & Smith, 1981; Douglas & Leslie, 1986; Clutton-Brock *et al.*, 1987; Albon & Clutton-Brock, 1988). The potential interactive effects of weather and population density on juvenile survival are of great interest from applied and theoretical viewpoints. Wildlife managers must incorporate these interactions in population models to make realistic forecasts of population changes, yet the necessary data are seldom available. Long-term investigations of the effects of weather and density are

particularly important because of controversy over the relative importance of density-dependent and density-independent variables in affecting population dynamics of ungulates (Caughley & Krebs, 1983; Fowler, 1987; Owen-Smith, 1990). Although several authors have suggested that weather and density may interact in affecting population dynamics of ungulates, and juvenile survival in particular (Sauer & Boyce, 1983; Picton, 1984; Douglas & Leslie, 1986; Owen-Smith, 1990), no study has explicitly tested for interactions between population density and weather variables. Density–climate interactions are particularly relevant to the study of population dynamics. It is generally believed that the effects of weather should be more evident near ecological carrying capacity (Picton, 1984; Strong, 1984; Sinclair, 1989), but hypotheses about interactions between density and weather are difficult to test for wild mammals because they require data from years of good

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and bad weather at high and low population density. Furthermore, as many researchers have pointed out (Clutton-Brock *et al.*, 1987; Forrester, 1995), density effects are not necessarily linear, and may be evident only when density exceeds a threshold. Current knowledge of ungulate population dynamics is limited not by the lack of theories and models, but by the availability of data (Sauer & Boyce, 1983; Eberhardt, 1985). Caughley (1981) and Sinclair (1989) pointed out the need to manipulate density to assess density-dependent effects on population dynamics of wild ungulates.

We used data from a long-term investigation of the bighorn sheep (*Ovis canadensis*) population at Ram Mountain, Alberta, to assess the effects of weather and population density on lamb survival. Because of an experimental manipulation of density (Jorgenson, Festa-Bianchet & Wishart, 1993b), the number of adult females in our study population more than tripled, providing the opportunity to assess the effects of weather under widely different levels of density. In addition, the unique characteristics of this study allowed us to separate neonatal and winter survival of lambs. We therefore avoided the confusion of pregnancy rate and early juvenile survival typical of studies that measure juvenile survival through female/offspring ratios (Picton, 1984; Douglas & Leslie, 1986).

The Canadian Rocky Mountains have long winters with deep snow and very cold temperatures. Although winter weather could affect the survival of bighorn lambs, weather during spring may also play an important role. Winter weather could have a direct effect on survival by increasing the costs of thermoregulation and by limiting access to vegetation through deep snow (Barrett, 1982; Burles & Hoefs, 1984; Van Ballenberghe, 1985; McLean, 1989; Gaillard *et al.*, 1993), but weather during spring may affect forage growth and could have immediate and delayed effects on juvenile survival, by affecting their nutrition and the ability of mothers to complete gestation and produce milk (Albon & Clutton-Brock, 1988; Albon, Clutton-Brock & Guinness, 1987; Festa-Bianchet, 1988b). Alpine and northern environments are characterized by a brief season of vegetation growth and many months when the vegetation is dormant and of poor nutritional quality (Festa-Bianchet, 1988d; Forchhammer, 1995). If spring weather affects vegetation growth, then it should have important consequences for nutrition, mass accumulation and survival of ungulates in environments with a very short growing season.

We expected a direct negative effect of cold and snowy winters on lamb survival during winter, and a delayed effect on neonatal survival of lambs born the following spring through a possible effect on maternal condition (Verme, 1977). We also expected a positive effect of warm and rainy springs upon neonatal and winter survival, because of direct effects on thermoregulation of new-born lambs (Geist, 1971) and delayed effects through weather impact on vegetation growth. We predicted that all weather effects on survival should be stronger at high population density, when per capita resources were scarcer as suggested by a later age of first reproduction, lower survival of yearling females, and decreased horn growth of adult males (Jorgenson *et al.*, 1993a, b, 1997).

MATERIALS AND METHODS

Study area

Ram Mountain, Alberta, Canada (52°N, 115°W), is an isolated outcrop separated from the main Rocky Mountain Range by about 30 km of foothills covered with coniferous forest. Bighorn sheep used approximately 38 km^2 of alpine and subalpine areas at elevations ranging from 1700 to 2200 m. The weather at Ram Mountain is harsh and unpredictable, with considerable day-to-day and year-to-year variations. It is marked by a wide yearly temperature range (40 °C between average daily summer high and winter low) coupled with moderate but variable annual precipitation (average of 637 mm, annual range from 452 to 804 mm). Temperatures of less than −40° can occur from December to March, and snowfalls have been recorded during all months of the year. Snow cover above 2000 m usually persists from November to May, but wide variations are possible. We usually opened our research camp (at about 1900 m) in late May: in some years there was no snow left, in others there was almost 2 m of snow.

Bighorn sheep population

Data used in this study were collected from 1975 to 1996. Until 1981, the population was kept at low density (about 30 adult ewes) through yearly removals of ewes. The herd increased to 104 adult ewes in 1992 and then gradually decreased to 73 in 1996 (Fig. 1), probably because of lower lamb survival (see 'Results') and later age of primiparity (Jorgenson *et al.*, 1993a). Sheep were captured from late May to early October in a corral trap baited with salt. Since 1976, all adult ewes have been individually marked with canvas collars. For adult females, resighting probability is over 99% (Jorgenson *et al.*, 1997), and because yearlings remain within ewe groups the resighting probability for lambs that survive the winter should be about the same. There has never been a sheep not seen as a yearling but later resighted. Therefore, we assumed that all bighorns seen as lambs and not seen as yearlings died during winter.

Most ewes were captured 2–5 times each summer. In most years, over 80% of the ewes were captured by the second week of June, as sheep are particularly attracted to salt in late spring. The trap could be shut directly from the field crew's living quarters, and it was operational on most days. We weighed and measured any captured ewe that had not been processed for 3 weeks or longer. Most lambs are born in the last 2 weeks of May, with a few born as late as early July. Reproductive
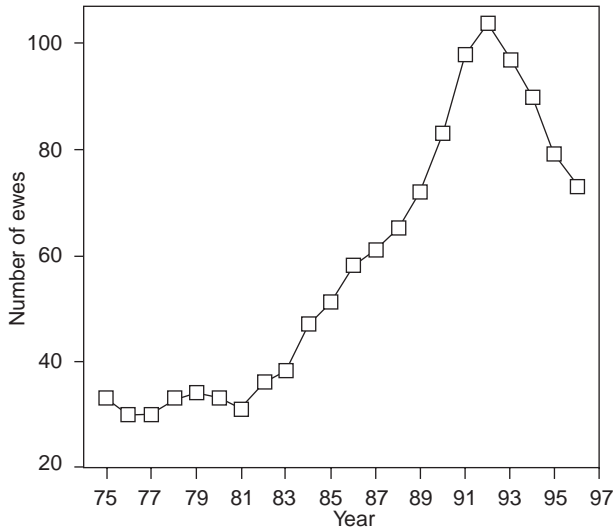
Fig. 1. Number of bighorn sheep females 2 years of age and older on Ram Mountain, Alberta, Canada from 1975 to 1996.

status of ewes was assessed by direct inspection of the udder at each capture and by observations of ewe–lamb associations in the field. We knew the total number of lambs born because we could account for the reproductive status of all ewes in the population. In most years, we captured and marked over 80% of the lambs, so that by September we had a very accurate count of the total number of lambs alive at the end of the summer. More details on the study area, capture, and observation methods are provided in Jorgenson *et al.* (1993*b*) and Bérubé, Festa-Bianchet & Jorgenson (1996).

We distinguished 3 phases of lamb mortality. Neonatal mortality refers to when examination of the udder at capture revealed that the ewe had produced a lamb (milk or colostrum were secreted), but the lamb was not seen. We suspect most of this mortality took place at birth or within a few days of birth, and, typically, the ewe had stopped producing milk by the next capture. Winter mortality was measured as the difference between the number of lambs alive in September and the number of yearlings the following May. In most years, all yearlings were marked by the end of June. Some lambs disappeared during summer. Summer mortality was relatively unimportant, averaging only 8% a year (compared to 17% for neonatal mortality and 28% for winter mortality). We therefore did not analyse data on summer mortality.

We rarely knew the proximate causes of lamb deaths, because less than 1% of carcasses were found. Predators such as cougars (*Puma concolor*), wolves (*Canis lupus*) and golden eagles (*Aquila chrysaetos*) were present, but we do not know how much mortality was due to predation.

Weather data

Weather data were collected by Environment Canada at the Nordegg meteorological station, about 20 km west of Ram Mountain at 1326 m elevation. Because of gaps in weather data collection, we could only use 16 years of data during 1975–1996.

To assess the effects of weather on lamb survival, we selected weather variables and seasons that appeared relevant from a biological viewpoint. The 3 measures of temperature available (daily minimum, daily maximum, and daily average) were closely correlated, and we selected daily maximum to measure variations in temperature because this value should be less subject to temperature inversion than minimum and average temperatures. The weather station is located in a valley and therefore temperature inversions are possible, particularly during winter.

In alpine habitats, precipitation and temperature in the growing season are positively correlated with primary production and with vegetation quality (Hoefs, 1984). In alpine ranges in Alberta, vegetation growth peaks in mid-June (Festa-Bianchet, 1988*d*), therefore we calculated average daily maximum temperature and total precipitation from 15 May to 15 June each year. Using precipitation data for the entire summer (mid-May to mid-August) always produced similar results to those of the period from mid-May to mid-June, which had greater explanatory power than precipitation over the entire summer. We related spring weather to neonatal survival and to survival during the following winter, because we hypothesized a delayed effect of spring nutrition upon lamb winter survival.

Snow cover has a negative effect on the foraging efficiency of bighorn sheep (Goodson, Stevens & Bailey, 1991) and could increase vulnerability to predators (Picton, 1984). Low winter temperatures could impose a direct energetic cost that could affect winter survival (Albon & Clutton-Brock, 1988). We calculated average temperature and amount of snowfall from 1 December to 31 March to test if harsh winter weather had a negative effect on lamb survival. Harsh winter weather during gestation may influence juvenile survival in ungulates (Verme, 1977), therefore we compared winter weather to winter survival of one cohort and neonatal survival of the subsequent cohort.

Statistical analysis

In bighorn sheep, as in most dimorphic ungulates, the sexes are segregated through most of the year. Ewes and rams tend to use different areas (Geist, 1971), therefore the amount of resources available to lambs should not depend on ram numbers. Consequently, we used the number of adult females (2 years and older) to measure population density.

We used logistic regression models (Agresti, 1990) to analyse survival, with female density and the previously defined climatic variables as explanatory variables. These variables were standardized (subtracting the mean and dividing by the standard deviation) so that regression coefficients were measured on a comparable scale, and therefore directly comparable. Standardization

does not affect significance tests or model selection. We assumed throughout a logit link between survival and the explanatory variables, as other links did not provide a better fit.

We fitted logistic regression models including additive effects of density and climate as well as their interactions (defined below). The fit of the model including all variables was assessed using a global goodness of fit test based on the deviance and on residual plots (Agresti, 1990). Variables were then removed one at a time, based on the Akaike Information Criterion or AIC (Christensen, 1990; Burnham & Anderson, 1992; Burnham, White & Anderson, 1995). The AIC is defined as the deviance +2*p, where p is the number of parameters of the model. This is a backward selection procedure implemented in S-plus for Windows, version 3.3 (Statistical Sciences, 1995). We used AIC instead of likelihood ratio (LR) significance tests because of the problems associated with multiple testing and because AIC seems to be more efficient at selecting a good model for inference (Anderson, Burnham & White, 1994; Burnham et al., 1995). We nevertheless provide the resulting change in deviance (and the associated LR tests). As all variables or interactions (see below) were continuous, LR tests were based on one degree of freedom, and a simpler model was better according to the AIC if the reduction in deviance was larger than 2.

Interactions between density and weather variables were defined as a product of standardized female density and each climatic variable, and the fit of the resulting model was used as a criterion to assess the need to use more complicated terms (Selvin, 1996). Multiplicative terms may not capture all the possible complexity of the interaction between density and climate, but they are the simplest way of defining non-additive effects.

For each selected model, we measured the explained variation using squared Pearson correlation between predicted values and observed values, as recommended by Mittlböck & Schemper (1996). There are many different ways of defining explained variation for binary data (Efron, 1978; Cox & Wermuth, 1992), but the measure we selected is the easiest to interpret and is nearly identical to other measures such as the proportion of residual sum of squares explained by the model. The squared Pearson correlation could be calculated at the individual level, or at the population level (see Cox & Wermuth, 1992 for a discussion). In the former case, the observed values are 0 or 1, and we measure the ability of the model to predict survival of a given individual. In the latter case, the observed values are the proportion surviving in a given year, and we measure the explained variation at the population level. Explained variation at the population level is always much higher than at the individual level because individual values are constrained to 0 or 1, while population values may take any value between 0 and 1 (Cox & Wermuth, 1992).
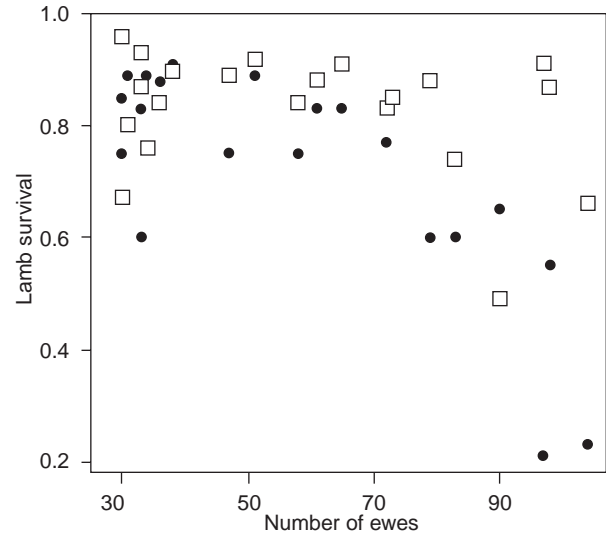

Fig. 2. Neonatal (open squares) and winter (closed circles) survival of bighorn sheep lambs at Ram Mountain, 1975 to 1996, compared to the number of adult ewes in the population in June of each year. Winter survival data are only available up to 1995.

RESULTS

The correlations between climatic variables and the number of females were low, the coefficients of determination were < 0.13 for winter survival and < 0.22 for neonatal survival. Considering all years from 1975 to 1995, mean neonatal survival calculated while accounting for yearly differences in sample size (see Burnham et al., 1987) was 0.841 (CV = 0.103), while mean winter survival of lambs was 0.727 (CV = 0.253) (Fig. 2).

Neonatal survival

The model including density and all four weather variables did not fit the data well (deviance = 30.71, $d.f. = 10$, $P = 0.0007$). Inspection of the residuals showed this was not due to outlying observations. We therefore considered a model with multiplicative effects between density and weather. The fit of the most complex model was not good (deviance = 13.27, $d.f. = 6$, $P = 0.039$), mainly due to the inclusion of unnecessary terms. Thus, multiplicative effects between density and snowfall ($\chi^2 = 0.127$, $d.f. = 1$, $P = 0.72$), multiplicative effects between density and spring precipitation ($\chi^2 = 0.995$, $d.f. = 1$, $P = 0.32$), and the effect of snowfall ($\chi^2 = 0.084$, $d.f. = 1$, $P = 0.77$) were not required. By removing these terms, we obtained a model with a better fit to the data (deviance = 14.48, $d.f. = 9$, $P = 0.11$). The remaining terms included spring precipitation ($\chi^2 = 7.16$, $d.f. = 1$, $P = 0.0075$), multiplicative effects of density and spring temperature ($\chi^2 = 13.0$, $d.f. = 1$, $P = 0.0003$) and multiplicative effects of density and winter temperature

($\chi^2 = 6.19$, $d.f. = 1$, $P = 0.013$). Thus, independently of other factors, spring precipitation had a positive effect on neonatal survival (slope 0.49 ± 0.18), while the positive effects of spring temperature (slope 0.33 ± 0.15) and, to a lesser extent, winter temperature (slope 0.13 ± 0.16) were only detectable at high density. We found no significant direct effect of density on neonatal survival (slope -0.03 ± 0.18). Density only affected neonatal survival by increasing the negative effects of unfavourable spring weather. Overall, the selected model explained 70% of the variation in neonatal survival at the population level (Fig. 3).

Winter survival

The model including population density and all four weather variables fitted the data well (deviance = 10.23, $d.f. = 10$, $P = 0.42$). Winter temperature ($\chi^2 = 1.70$, $d.f. = 1$, $P = 0.19$) and snowfall ($\chi^2 = 1.05$, $d.f. = 1$, $P = 0.31$) had no significant effects on winter survival of bighorn lambs. On the other hand, density ($\chi^2 = 28.71$, $d.f. = 1$, $P < 0.0001$), previous spring temperature ($\chi^2 = 11.11$, $d.f. = 1$, $P = 0.001$) and previous spring precipitation ($\chi^2 = 6.31$, $d.f. = 1$, $P = 0.012$) accounted for a significant proportion of the yearly variation in lamb winter survival, explaining 84% of this variation at the population level (Fig. 3). Models including multiplicative terms did not fit the data better (deviance = 13.02, $d.f. = 12$, $P = 0.37$; multiplicative effects of density and spring temperature: $\chi^2 = 0.05$, $d.f. = 1$, $P = 0.82$; multiplicative effects of density and spring precipitation: $\chi^2 = 2.35$, $d.f. = 1$, $P = 0.13$). There was, therefore, no statistical evidence of an interaction between weather and density. As expected, lamb survival was negatively correlated with density (slope -0.61 ± 0.11) and positively correlated with spring temperature (slope 0.45 ± 0.13) and precipitation (slope 0.36 ± 0.14).

DISCUSSION

We expected that lamb survival would be negatively affected by population density and that any effects of weather on lamb survival would be most evident at high density. The results of our analyses generally confirmed our expectations, but highlighted the different effects of density, weather, and weather–density interactions upon different phases of lamb survival. Our study provides conclusive evidence that winter survival of bighorn lambs in the Ram Mountain population is density-dependent. Population density also had an indirect negative effect on neonatal survival, by making newborn lambs more likely to die when the weather was unfavourable. Our results exemplify the value of accurate long-term data in understanding the dynamics of ungulate populations and underline the key role played by spring weather in affecting survival of bighorn lambs.

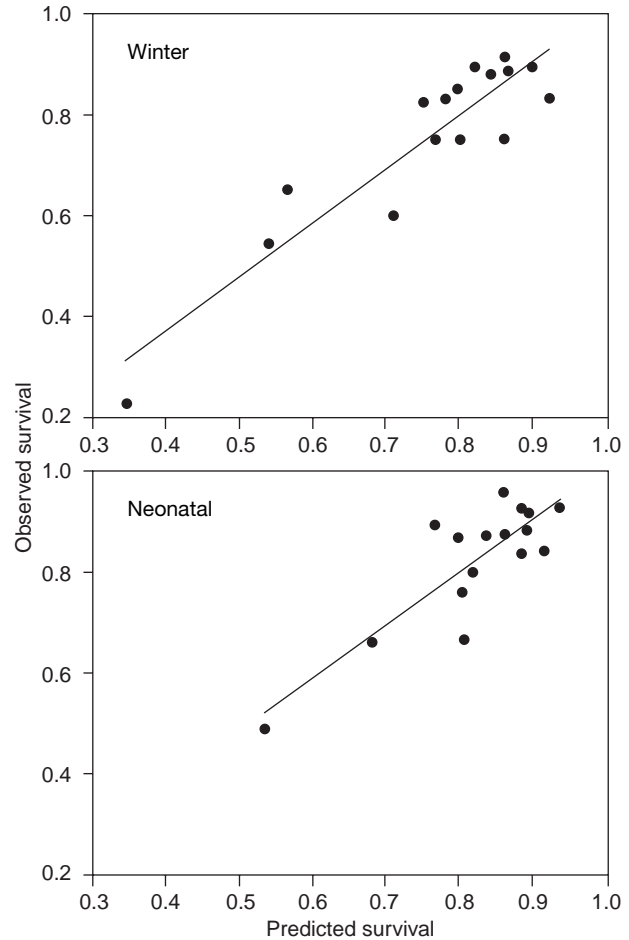The survival of bighorn sheep aged one year of age

Fig. 3. Observed neonatal and winter survival of bighorn sheep lambs at Ram Mountain compared with the survival predicted by the final models.

and older at Ram Mountain is independent of population density with the exception of yearling females, whose survival decreased at high density (Jorgenson et al., 1997). The strong density-dependence in survival shown by lambs in this population agrees with other studies of ungulates that have generally found that juveniles are more sensitive to resource availability than adults (Fowler, 1987). We probably found clear density-dependence in this population because we examined juvenile survival over a wide range of population densities: the number of adult ewes more than tripled during our study (Fig. 1). Although we did not directly measure vegetation productivity or biomass, several lines of evidence suggest that the Ram Mountain population was limited by food availability. At high density, age of primiparity (Jorgenson et al., 1993a) and mortality of yearling females increased (Jorgenson et al., 1997), while horn growth of males (Jorgenson et al., 1993b) and lamb survival decreased (this study). The survival of adult females was independent of population density (Jorgenson et al., 1997), but lower lamb survival and later age of primiparity apparently depressed recruitment to the point that the population decreased

(Fig. 1). Density-dependent effects are not found in all bighorn sheep populations. For example, in the Sheep River population the number of sheep appear to be limited by disease and predation (Festa-Bianchet, 1988*c*; Ross, Jalkotzy & Festa-Bianchet, 1997). Lamb survival at Sheep River has been density-independent (comparing winter survival of lambs with the number of ewes from 1982 to 1995: analysis of deviance, $F_{1,13} = 0.58$, $P = 0.46$), probably because population density at Sheep River never reached a point where resources were scarce enough to affect population processes. During our studies, the number of ewes in the Ram Mountain population more than tripled, but at Sheep River it only ranged from 44 to 71. Age of primiparity was density-dependent at Ram Mountain but not at Sheep River (Jorgenson *et al.*, 1993*a*).

In analyses of population dynamics, weather is classically considered a density-independent effect (Owen-Smith, 1990), but our results show that complex weather–density interactions can affect juvenile survival in ungulates. Some weather effects were indeed independent of population density: wet springs always had a positive effect on lamb survival, and warm springs increased lamb survival during the following winter. However, warm temperatures in winter and spring had positive effects on neonatal survival at high density, while at low population density temperature had no effect on neonatal survival. Therefore, while obviously weather and population density are not causally linked, not all weather variables have strictly density-independent effects on population dynamics. This finding underlines the difficulties of predicting juvenile survival in bighorn sheep and possibly in other ungulates.

Geist (1971), based on a survey of the domestic sheep literature, predicted that survival of bighorn lambs should be affected by inclement weather near the time of birth. That prediction was generally accepted, despite the scarcity of data relating bighorn lamb survival to weather during parturition. We found that neonatal survival was higher in years with wet springs at all levels of population density, possibly because of a positive effect of spring precipitation on vegetation growth. At high density, neonatal survival was higher if the previous winter and the spring were warm. Mothers may have been weakened by lack of food and therefore sensitive to any additional demands on their energy budget, such as those imposed by low winter temperatures. Cold spring weather may have had a direct adverse effect on neonatal survival at high density as new-born lambs may have been weak because of poor maternal condition during gestation. In addition, cold weather in spring probably delayed vegetation growth and had a negative effect on the mother's nutrition. Maternal nutrition affects neonatal survival in several ungulate species (Verme, 1977; Leader-Williams, 1980; Clutton-Brock *et al.*, 1987). The several consecutive years of high population may have had a cumulative adverse impact on vegetation and indirectly on maternal condition, increasing the possibility that inclement weather reduced lamb survival.

Unlike neonatal survival, the effects of weather on winter lamb survival did not vary with population density. Surprisingly, however, winter lamb survival was affected by weather during the previous spring and not by winter weather. Spring temperature and precipitation presumably affected vegetation quality and quantity, which in turn may affect the amount of reserves accumulated by lambs during summer, and their ability to survive the winter. Poor vegetation growth could negatively affect lamb mass gain directly, by decreasing the quantity or quality of the forage they eat, and, indirectly, by decreasing their mother's ability to produce sufficient milk (Festa-Bianchet, 1988*b*). At high density, mothers gained as much mass during summer as at low density, but the mass gain by lambs decreased, suggesting a lower level of maternal expenditure (Festa-Bianchet & Jorgenson, 1998): it is possible that mothers further reduced their level of care when weather conditions were unfavourable. Winter survival of bighorn lambs at Ram Mountain increases with body mass in mid-September, and lamb mass decreased as density increased (Festa-Bianchet *et al.*, 1997). At Sheep River, late-born lambs that enter the winter in a retarded state of development experience very high mortality (Festa-Bianchet, 1988*a*). Small lambs could be more vulnerable to starvation (Bartmann, White & Carpenter, 1992). Small lambs could also be weak and more susceptible to predation than larger lambs, but results from a study of cougar predation on bighorn lambs at Sheep River (Ross *et al.*, 1997) do not suggest that small lambs are selected as prey.

Despite the harshness and variability of winter weather, in this study we observed no correlation between snowfall or winter temperature and winter lamb survival. Total snowfall may not be a very relevant weather variable, because bighorn sheep winter ranges are often located in areas where snow cover is short-lived. Chinook winds melt the snow at low elevations and clear it from higher slopes, while snowslides remove snow from steep grazing areas. Northern ungulates have numerous adaptations to harsh winter weather: food requirements are reduced during winter by lowering metabolic rate and decreasing food intake (Heydon *et al.*, 1993; Walkden-Brown, Norton & Restall, 1994). In bighorn sheep, the thermoneutral zone in winter extends to $-20\,°C$ (Chappel & Hudson, 1978): above this temperature no additional energy expenditure is required to resist the effects of cold weather. We suggest that only exceptionally cold and long winters, worse than any encountered during our study, may affect the survival of mountain sheep (Burles & Hoefs, 1984). Spring weather, however, has an indirect effect on winter survival of bighorn lambs, presumably by affecting body reserves at the onset of winter. Our results therefore join those of Clutton-Brock *et al.* (1987) and Gaillard *et al.* (1996) in underlying the importance of spring weather for the growth and survival of juvenile ungulates in northern environments.

Acknowledgements

REFERENCES

Albon, S. D. & Clutton-Brock, T. H. (1988). Climate and the population dynamics of red deer in Scotland. In *Ecological change in the Uplands*: 93–107. Usher, M. B. & Thompson, D. B. A. (Eds). Oxford: Blackwell Scientific Publications.

Albon, S. D., Clutton-Brock, T. H. & Guinness, F. E. (1987). Early development and population dynamics in red deer. II. Density-independent effects of cohort variation. *J. Anim. Ecol.* **56:** 69–81.

Agresti, A. (1990). *Categorical data analysis*. New York: John Wiley & Sons.

Anderson, D. R., Burnham, K. P. & White, G. C. (1994). AIC model selection in overdispersed capture-recapture data. *Ecology* **75:** 1780–1793.

Barrett, M. W. (1982). Distribution, behavior and mortality of pronghorns during a severe winter in Alberta. *J. Wildl. Manage.* **46:** 991–1002.

Bartmann, R. M., White, G. C. & Carpenter, L. H. (1992). Compensatory mortality in a Colorado mule deer population. *Wildl. Monogr.* **121:** 1–39.

Bérubé, C., Festa-Bianchet, M. & Jorgenson, J. T. (1996). Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. *Behav. Ecol.* **7:** 60–68.

Burles, D. W. & Hoefs, M. (1984). Winter mortality of Dall sheep, *Ovis dalli dalli*, in Kluane National Park, Yukon. *Can. Field-Nat.* **98:** 479–484.

Burnham, K. P. & Anderson, D. R. (1992). Data-based selection of an appropriate biological model: the key to modern data analysis. In *Wildlife 2001: populations*: 16–30. McCullough, D. R. & Barrett, R. H. (Eds). London, U.K.: Elsevier Science Publishers.

Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C. & Pollock, K. H. (1987). *Design and analysis methods for fish survival experiments based on release-recapture. Am. Fish. Soc. Monogr.* No. 5. Bethesda, Maryland.

Burnham, K. P., White, G. C. & Anderson, D. R. (1995). Model selection strategy in the analysis of capture-recapture data. *Biometrics* **51:** 888–898.

Caughley, G. (1981). Comments on natural regulation of ungulates (what constitutes a real wilderness?). *Wildl Soc. Bull.* **9:** 232–234.

Caughley, G. & Krebs, C. J. (1983). Are large mammals simply small mammals writ large? *Oecologia* **59:** 7–17.

Chappel, R. W. & Hudson, R. J. (1978). Winter bioenergetics of Rocky Mountain bighorn sheep. *Can. J. Zool.* **56:** 2388–2393.

Christensen, R. (1990). *Log-linear models*. New York: Springer-Verlag.

Clutton-Brock, T. H., Major, M., Albon, S. D. & Guinness, S. D. (1987). Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *J. Anim. Ecol.* **56:** 53–67.

Cox, D. R. & Wermuth, N. (1992). A comment on the coefficient of determination for binary responses. *Am. Statist.* **46:** 1–4.

Douglas, C. L. & Leslie, D. M. (1986). Influence of weather and density on lamb survival of desert mountain sheep. *J. Wildl. Manage.* **50:** 153–156.

Eberhardt, L. L. (1985). Assessing the dynamics of wild populations. *J. Wildl. Manage.* **49:** 997–1012.

Efron, B. (1978). Regression and ANOVA with zero-one data: measures of residual variation. *J. Am. Statist. Assoc.* **73:** 113–121.

Festa-Bianchet, M. (1988a). Birthdate and survival in bighorn lambs (*Ovis canadensis*). *J. Zool. (Lond.)* **214:** 653–661.

Festa-Bianchet, M. (1988b). Nursing behaviour of bighorn sheep: correlates of ewe age, parasitism, lamb age, birthdate and sex. *Anim. Behav.* **36:** 1445–1454.

Festa-Bianchet, M. (1988c). A pneumonia epizootic in bighorn sheep, with comments on preventive management. *Biennial Symposium of the Northern Wild Sheep and Goat Council* No. 6: 66–76.

Festa-Bianchet, M. (1988d). Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia* **75:** 580–586.

Festa-Bianchet, M. & Jorgenson, J. T. (1998). Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behav. Ecol.* **9:** 144–150.

Festa-Bianchet, M., Jorgenson, J. T., Bérubé, C. H., Portier, C. & Wishart, W. (1997). Body mass and survival of bighorn sheep. *Can. J. Zool.* **75:** 1372–1379.

Forchhammer, M. C. (1995). Sex, age, and seasonal variation in the foraging dynamics of muskoxen, *Ovibos moschatus*, in Greenland. *Can. J. Zool.* **73:** 1344–1361.

Forrester, G. F. (1995). Strong density-dependence survival and recruitment regulate the abundance of coral reef fish. *Oecologia* **103:** 275–282.

Fowler, C. W. (1987). Density dependence in large mammals. In *Current mammalogy*: 401–441. Genoways, H. H. (Ed.). New York: Plenum Press.

Fowler, C. W. & Smith, T. D. (1981). *Dynamics of large mammals populations*. New York: Wiley.

Gaillard, J.-M., Delorme, D., Boutin, J.-M., Laere, G. V. & Boisaubert, B. (1996). Body mass of roe deer fawns during winter in 2 contrasting populations. *J. Wildl. Manage.* **60:** 29–36.

Gaillard, J.-M., Delorme, D., Boutin, J.-M., Laere, G. V., Boisaubert, B. & Pradel, R. (1993). Roe deer survival patterns: a comparative analysis of contrasting populations. *J. Anim. Ecol.* **62:** 778–791.

Geist, V. (1971). *Mountain sheep*. Chicago: University of Chicago Press.

Goodson, N. J., Stevens, D. R. & Bailey, J. A. (1991). Effects of snow on foraging ecology and nutrition of bighorn sheep. *J. Wildl. Manage.* **55:** 214–222.

Gunn, A., Miller, F. L. & McLean, B. (1989). Evidence for and possible causes of increased mortality of bull muskoxen during severe winters. *Can. J. Zool.* **67:** 1106–1111.

Heydon, M. J., Sibbald, A. M., Milne, J. A., Brinklow, B. R. & Loudon, A. S. I. (1993). The interaction of food availability and endogenous physiological cycles on the grazing ecology of red deer hinds (*Cervus elaphus*). *Funct. Ecol.* **72:** 216–222.

Hoefs, M. (1984). Productivity and carrying capacity of a sub-arctic sheep winter range. *Arctic* **37:** 141–147.

Jorgenson, J. T., Festa-Bianchet, M., Gaillard, J.-M. & Wishart, W. D. (1997). Effects of age, sex, disease and density on survival of bighorn sheep. *Ecology* **78:** 1019–1032.

Jorgenson, J. T., Festa-Bianchet, M., Lucherini, M. & Wishart, W. D. (1993*a*). Effects of body size, population density and maternal characteristics on age of first reproduction in bighorn ewes. *Can. J. Zool.* **71:** 2509–2517.

Jorgenson, J. T., Festa-Bianchet, M. & Wishart, W. D. (1993*b*). Harvesting bighorn ewes: consequences for population size and trophy ram production. *J. Wildl. Manage.* **57:** 429–435.

Leader-Williams, N. (1980). Population dynamics of reindeer introduced into South Georgia. *J. Wildl. Manage.* **44:** 640–657.

Mittlböck, M. & Schemper, M. (1996). Explained variation for logistic regression. *Statist. Med.* **15:** 1987–1997.

Owen-Smith, N. (1990). Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. *J. Anim. Ecol.* **59:** 893–913.

Picton, H. D. (1984). Climate and the prediction of reproduction of three ungulate species. *J. Appl. Ecol.* **21:** 869–879.

Ross, P. I., Jalkotzy, M. G. & Festa-Bianchet, M. (1997). Cougar predation on bighorn sheep in southwestern Alberta. *Can. J. Zool.* **75:** 771–775.

Sauer, J. R. & Boyce, M. S. (1983). Density dependence and survival of elk in northwestern Wyoming. *J. Wildl. Manage.* **47:** 31–37.

Selvin, S. (1996). *Statistical analysis of epidemiologic data*. New York: Oxford University Press.

Sinclair, A. R. E. (1977). *The African buffalo*. Chicago: University of Chicago Press.

Sinclair, A. R. E. (1989). Population regulation in animals. In *Ecological concepts*: 197–241. Cherrett, J. M. (Ed.). Oxford, U.K.: Blackwell Scientific Publications.

Statistical Sciences (1995). *S-plus guide to statistical and mathematical analysis, version 3.3*. Seattle: StatSci, Mathsoft, Inc.

Strong, D. R. (1984). Density-vague ecology and liberal population regulation in insects. In *A new ecology*. Price, P. W., Slobodchikoff, C. N. & Gaud, W. S. (Eds). New York: John Wiley & Sons.

Van Ballenberghe, V. (1985). Wolf predation on caribou: the Nelchina herd case history. *J. Wildl. Manage.* **49:** 711–720.

Verme, L. J. (1977). Assessment of natality mortality in upper Michigan deer. *J. Wildl. Manage.* **41:** 700–708.

Walkden-Brown, S. W., Norton, B. W. & Restall, B. J. (1994). Seasonal variation in voluntary feed intake and growth in Cashmere bucks fed ad libitum diets of low or high quality. *Aust. J. Agric. Res.* **45:** 355–366.