

# The implications of environmental variability on caribou demography: theoretical considerations

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*Abstract:* Random environmental influences, such as snow cover, are widely regarded as an integral feature of caribou population dynamics. We conducted computer simulations to explore the ramifications of such stochastic variability for caribou demography. We devised 4 models with increasing levels of complexity: Model 1, density-independence under different levels of stochasticity and  $r$ ; Model 2, non-linear effect of snow cover on  $r$ ; Model 3, non-linear effect of snow cover on  $r$  and stochasticity as a function of population size; and Model 4, non-linear effect of snow cover on  $r$ , stochasticity as a function of population size, and density-dependence according to the logistic equation. The results of Model 1 indicated that nearly all caribou populations subject only to environmental vagaries experienced either extinction or irruption. Model 2 revealed that non-linear effect of snow cover depressed the realised  $r$  as a function of population size. Finally, Model 4 suggested long-term population as previously reported in literature, but with reduced chance of overshooting  $K$  under moderate to high environmental variability.

**Keywords:** caribou demography, computer simulation, environmental variability, population dynamics.

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## Introduction

One of the axioms of population biology is that virtually no population fluctuates solely as a function of its density (Strong 1986). Indeed, random environmental changes, such as snow cover, are widely regarded as a prominent part of the population dynamics of caribou (Klein 1968, Reimers 1977, Gates *et al.* 1986, Melgaard 1986, Schaefer and Pruitt 1991). One approach to the study of environmental effects on population change is to control such effects either experimentally (e.g., Ollason 1977) or statistically (e.g., Botsworth 1985, Mech *et al.* 1987, Messier 1991a). A complementary approach is to construct strategic models (Nisbet and Gurney 1982) to generate new hypotheses.

Here, we report on the results of a series of such computer simulations to explore the ramifications of environmental vagaries on caribou demography. We began with a simple model of pure density-independence (Model 1) into which we incorporated increasing levels of complexity (Models 2-4). Our models are simple (there is no age structure, for example), and

thus it is the qualitative results that were of interest, inasmuch as they might be of heuristic value.

All simulations were conducted with SIMCON software (D. Vales and C.J. Walters, Univ. British Columbia, Vancouver, B.C.) using QuickBasic version 4.5 (MicroSoft Corp., Redmond, VA).

### *Model 1: Density-independence*

We began by simulating each model population through a simple, unlimited random walk. For each replicate population projected over 1000 years, we specified a mean value of  $r$  and a stochasticity factor in standard deviation (SD) units (Fig. 1). Fluctuations on  $r$  were normally distributed about the mean, with a SD varying from 0 to 0.5 of  $r_{\text{MAX}}$  (0.25).  $N_0$  was 50 for all cases. For each combination of  $r$  and SD, we calculated the likelihoods of extinction ( $N < 1$ ) and irruption ( $N > 1000$ ) for 1000 replicate populations.

The results indicated that the probabilities of extinction and irruption were sensitive to both

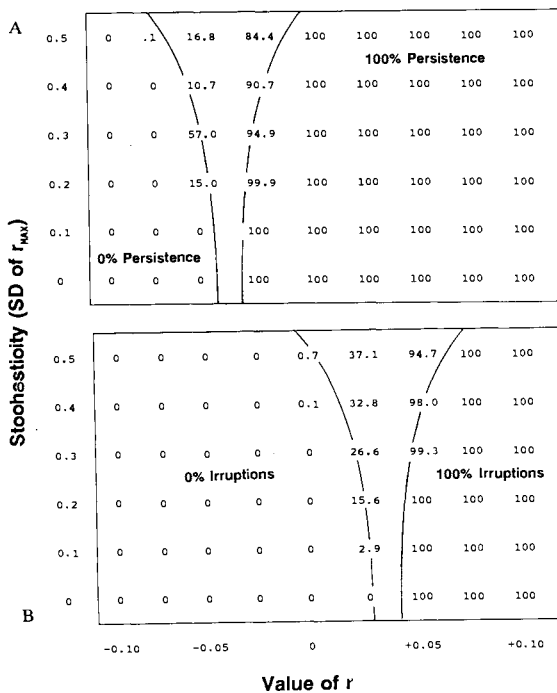


Figure 1. Probabilities (%) of (A) persistence ( $N > 1$ ) and (B) irruption ( $N > 1000$ ) under various combinations of  $r$  and stochasticity. Each datum represents 1000 replicate populations projected over 1000 years (mean  $r$  value and SD. The full model was  $N_{t+1} = N_t e^r$  where  $N$  represented population size, and  $r$  was a normally-distributed growth rate with a mean varying from -0.10 to +0.10 and a SD varying from 0 to 0.5 of  $r_{MAX}$  (0.25).

$r$  and stochasticity (Fig. 1). At low intrinsic growth rates, most populations were unable to persist; at high growth rates, persistence rates improved but most of these populations also irrupted. Persistence and irruption probabilities were more sensitive to stochasticity at intermediate  $r$  levels (-0.03 to +0.03).

Our results are consistent with earlier models (Leigh 1981, Belovsky 1987, Goodman 1987, Pimm *et al.* 1988, 1989) that persistence times increase with increasing  $r$  and with decreasing magnitude of temporal fluctuations. Pimm *et al.* (1988) confirmed these hypotheses empirically in a study of extinction rates of British birds.

These results further underline the distinction between factors which are *limiting*, producing annual fluctuations in density, and those which are *regulating*, maintaining densities within reasonable bounds (Murray 1982, Fowler 1987,

Messier 1991a,b). Regulating factors generate stabilisation of animal numbers and are necessary to ensure the numerical persistence of population. Our results reinforce the idea that in a solely density-independent world, any level of stochasticity, however slight, will ultimately cause population extinction or explosion.

This argument was recognised intuitively by Reddings (1971) and Strong (1986). These authors, while conceding its logic, countered by noting that it focuses on the ultimate result following an infinite amount of time. Thus Reddingus (1971:37) wrote: «It can never be observed that animal populations persist forever». Nonetheless, the narrow margin between extinction and unrealistic densities (compare Fig. 1A and 1B) implies that unbounded random walks are inadequate models for animal populations. Some form of density-dependence, or ceiling on density-independence («density-vagueness» of Strong 1984, 1986), is required for long-term population persistence.

#### Model 2: Non-linear effect of snow cover

In Model 1, we applied variability to  $r$  directly. In this and subsequent models, we specified a relationship between  $r$  and a random variable, snow cover. In particular, we visualised an ever-decreasing function such that each increment of snow accumulation had an increasingly depressing effect on  $r$  (Fig. 2). Snow cover was normally-distributed random variable (mean = 1, SD = 0.5). The postulated function (Fig. 2) was associated with a deterministic rate of growth

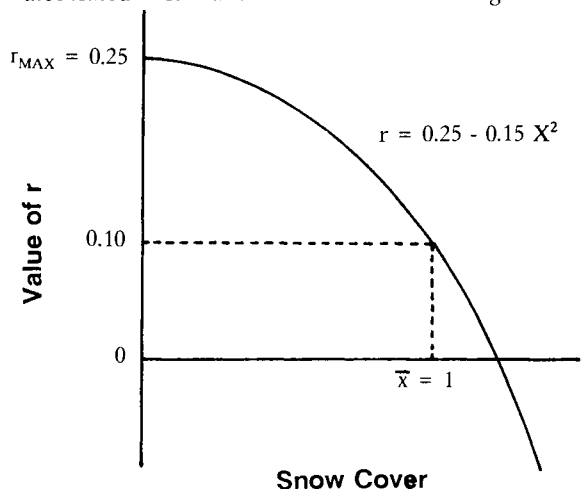


Figure 2. Hypothesised non-linear relationship between  $r$  and snow cover for Model 2. Snow cover values were normally distributed, with a mean of 1 and SD of 0.5.

( $r_{\text{DET}}$ ) of 0.10 for average snow cover, and  $r_{\text{MAX}}$  of 0.25 with no snow. These values were within the range of possible values reported in the literature for *Rangifer* (Bergerud 1980).

Although snow cover varied symmetrically about its mean, caribou population growth did not. Year-to-year variations in snow cover generated an average  $r$  value lower than that without variation. This was due to the non-linear relationship: an increment in snow cover above the mean negatively affected population growth more than the converse situation. Thus, the mean exponential rate of increase ( $r = 0.06$ ) with environmental variability was lower than the deterministic  $r$ -value ( $r_{\text{DET}} = 0.10$ ) under a constant environment (Fig. 3A). Consistent with this realised  $r$ , populations typically irrupted (Fig. 3B).

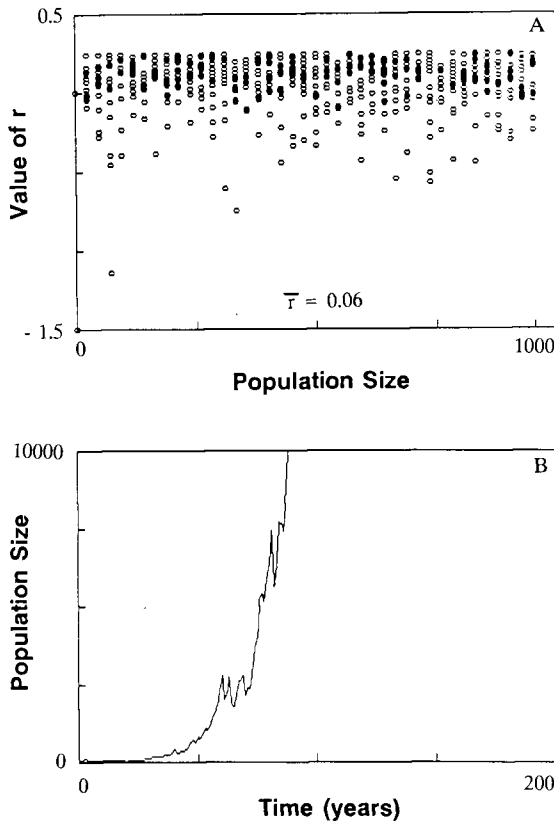


Figure 3. (A) Realised values of  $r$  at various densities as generated by Model 2. The full model was  $N_{t+1} = N_t e^{r(t)}$  where  $N$  represented population size and  $r$  (population growth rate) was a stochastic function of snow as depicted in Fig. 2. (B) Typical trajectory of a population under Model 2.

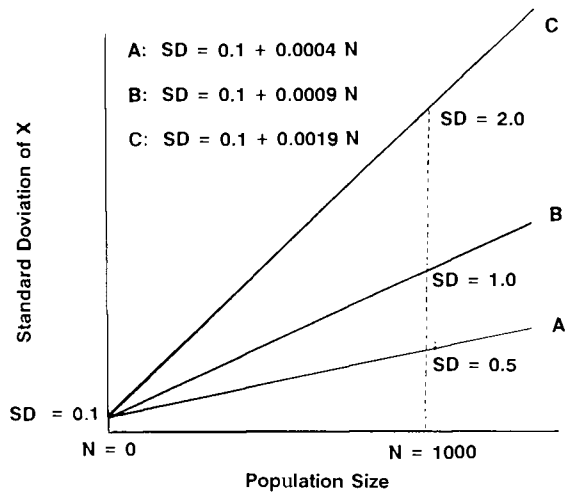


Figure 4. Hypothesised relationship between the level of stochasticity (SD of snow cover effect, X) and population size for (A) low, (B) medium, and (C) high levels of stochasticity.

This depression on population growth due to environmental variability accords with previous models of the demography of large, tropical herbivores. Van Sickle (1990) assumed that rainfall determined calf survival of African ungulates and found that long-term rates of population growth declined whenever such random variation was applied. Similarly, Caughley (1987) noted that symmetrical deviations in pasture biomass (driven by rainfall) produced a mean density of kangaroos lower than that in the absence of environmental variability. He hypothesised an analogous non-linear numerical response of the animals to an environmental parameter (pasture biomass) as we suggested in Fig 2. A discrepancy in deterministic and realised values, due to variability, is characteristic of such concave-down functions (Rubenstein 1982).

#### Model 3: Non-linear effect of snow cover, and stochasticity as a function of animal density

Here, we extended Model 2. We retained the non-linear relationship between snow cover and population growth (Fig. 2) and visualised a level of stochasticity as a linear function of population size (Fig. 4) rather than being fixed (i.e.,  $SD$  of snow = 0.5) as in Model 2. We explored three levels of such stochastic change, submodels A, B and C, each with increasing slopes of the stochasticity-density function.

What is the biological basis for this relationship between the level of stochasticity and density? We hypothesise that a higher population le-

vels, cratering by caribou may exacerbate the effect of snow cover such that subsequent foraging is impeded. This hypothesis follows Pruitt (1959) who noted the biologically important alteration in snow cover due to caribou cratering; consequently, animals typically do not excavate for terrestrial lichens more than twice in a given area. Figure 4 implies an interaction between the variability of the effect of snow cover and population densities of caribou. We hypothesise that food availability (not to be confused with food abundance) is a negative function of cratering intensity in a given environment. Caughley (1987) also reported a greater coefficient of variability for vegetation biomass in the presence of high numbers of kangaroos than in their absence.

As in Model 2, realised  $r$ -values were depressed compared to a deterministic  $r$ -value of 0.10. Here, however, the two facets of Model 3 combined such that population growth was density-dependent. At low densities ( $N = 50$ ), values close to  $r_{\text{DET}}$  were attained because environmentally-induced variability in  $r$  was minimal. At the other extreme ( $N = 1000$ ), depression of the population growth rate was greater for all three submodels (Fig 5). As expected, this decline was most severe for the high stochasticity submodel (Fig. 5C). This density-dependence, related to environmental variability, was reflected in the population trajectories (Fig. 6). Populations tended to persist within density bounds, often with precipitous declines from high densities. The high stochasticity submodel was characterised by lower densities and an apparently higher probability of extinction (Fig. 6C) due to the elevated chance of successive low values of  $r$  (Fig. 5C). We noted, however, that most population trajectories did not reveal predictable cyclicality in animal numbers.

The density relationships depicted in Fig. 5 are similar to Strong's (1986:260) «spreading scatters», a correlated mean and variance of  $r$ . Strong suggested that under such a scenario, populations will experience density-vagueness, i.e., density-dependent feedback only at high densities. Below some ceiling, fluctuations will be largely random, driven by stochastic effects. Although the magnitude of population declines was greater at higher densities (Fig. 6), population growth declined predictably with  $N$  (Fig. 5). Thus, the appearance of density-vagueness may simply coincide with a lack of detectability of regulating processes at low densities.

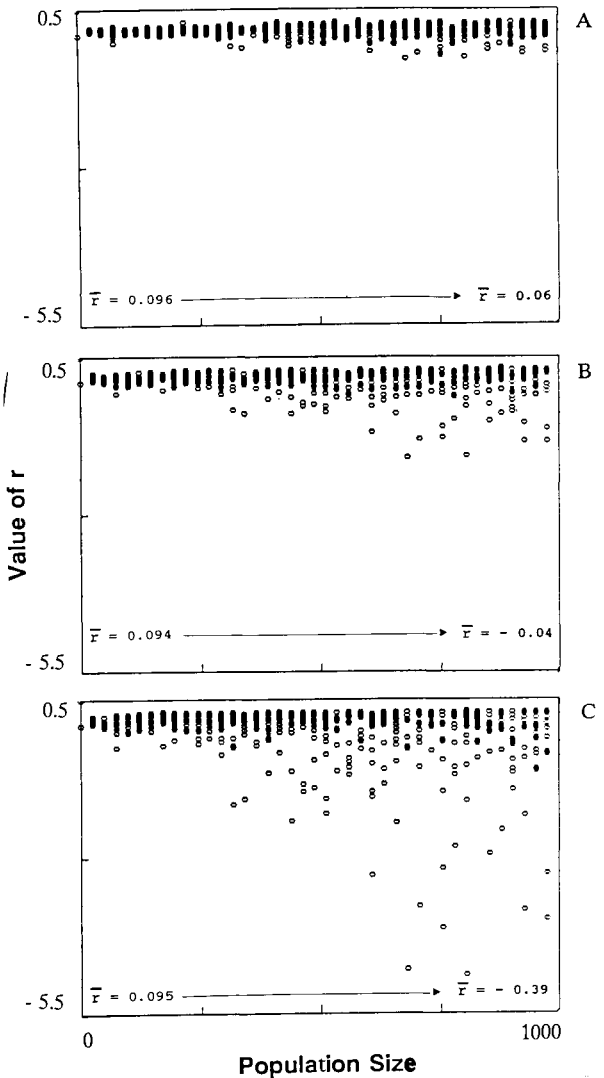


Figure 5. Realised values of  $r$  at various densities as generated by Model 3 for (A) low, (B) medium, and (C) high levels of stochasticity. Average  $r$ -values at  $N = 50$  and  $N = 1000$  are presented at the bottom of each panel to illustrate the predictable decline of  $r$  with increasing population size. The full model was  $N_{t+1} = N_t e^{r(s,N)}$  where  $N$  represented population size, and  $r$  (the population growth rate) was a stochastic function of snow cover effect as influenced by caribou numbers (see Fig. 2, 4). With no environmental variability,  $r$  was fixed at 0.10.

The decline in the growth rate of hypothetical populations, with increasing environmental variance, has been noted elsewhere (Tuljapurkar and Orzack 1980, Van Sickle 1990). If environ-

mental variability increases with population size (as we hypothesise), then our results imply that population regulation can be attained, specifically because the non-linear function depicted in Fig. 2 becomes more instrumental in depressing  $r$  at high population densities. In effect, the two components of Model 3 (the non-linear effect of snow and increasing variability with density) alter the year-to-year carrying capacity for caribou. This may fit Strong's (1986) notion of «liberal» population regulation where density bounds are unlikely to be static. Finally, our model is qualitatively consistent with observations of Meldgaard (1986) who noted that long-term population fluctuations of Greenland caribou were often dramatic, occasionally terminating in extinction.

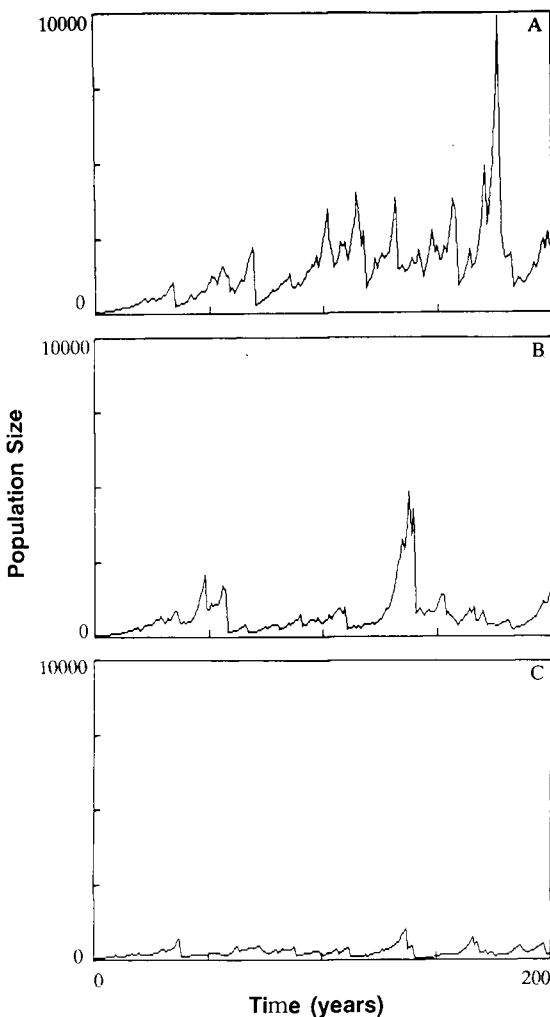


Figure 6. Typical trajectories for population under Model 3 for (A) low, (B) medium, and (C) high levels of stochasticity.

#### Model 4: Non-linear effect of snow cover, stochasticity as a function of animal density, and density-dependent logistic growth

Next, we explored the behaviour of hypothetical populations when our stochastic model was incorporated into a traditional logistic model. Model 4 thus specified two sources of depression on  $r$ : that caused by snow cover (Model 3) and that due to the logistic growth equation. We used a moderate level of stochasticity (equation B of Fig. 4), set carrying capacity<sup>†</sup> without snow ( $K$ ) at 400, and included 20-year time delay ( $T$ ) in the logistic growth equation as hypothesised by Messier *et al.* (1988). A  $r_{\text{DET}}$  of 0.10 and  $T$  of 20 resulted in density peak of  $3K$  for each population cycle (Fig. 7A) as previously reported by Messier *et al.* (1988).

The results of our simulations were variable. In some trajectories, the underlying cyclicity (typical of logistic models with time delays) was retained although obscured, with troughs somewhat elevated and peaks truncated (Fig. 7B) compared to the deterministic model. In others, population cycles were barely discernible (Fig. 7C). On occasion, the density-dependent time-delay and the immediate snow effect worked in tandem to produce rapid declines from high density. An interesting and general feature of Model 4 was that the chance of severely overshooting  $K$  was reduced appreciably with moderate to high environmental variability (e.g., Fig. 7B,C).

#### Conclusions

Our results imply two effects of snow caribou demography (Fig. 8). First, a density-independent effect, such that  $K$  with snow is less than  $K$  without snow. Second, a stabilising effect of snow as a consequence of the non-linear relationship between snow cover and  $r$  (Fig. 2), and the increase in variance of the snow cover effect with  $N$  (Fig. 4). This second influence may arise because caribou themselves affect the properties of snow cover, an interaction that may further depress population growth at high densities, in addition to any density-dependent resource limitations (Skogland 1985, 1986). Our Model 3, for example, infers no significant reduction in forage biomass *per se*, only in reduced access to forage resources in winter due to snow disturbance by caribou. In essence, this implies that  $K$  for caribou populations is not

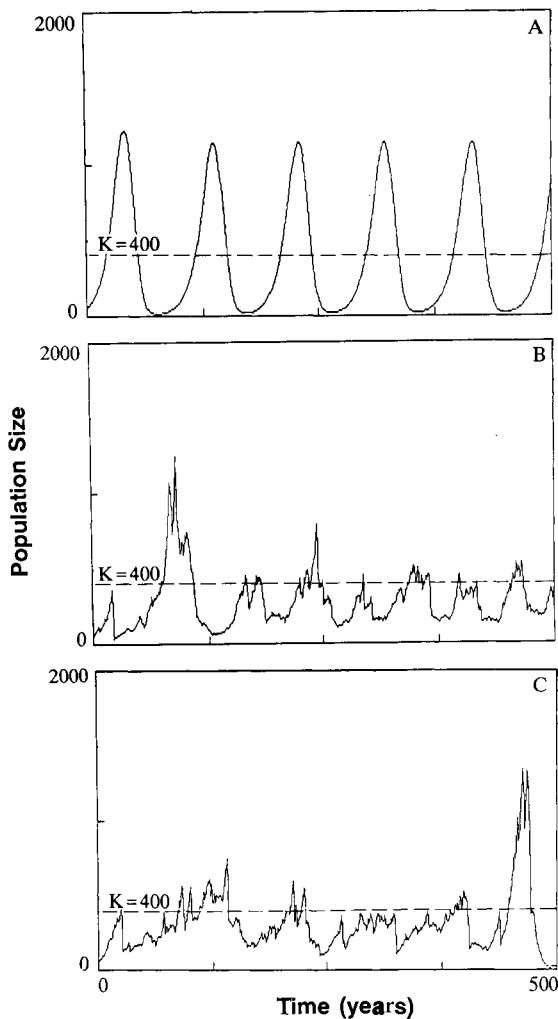


Figure 7. Typical population trajectories for (A) deterministic logistic growth and 20-year time delay (Messier *et al.* 1988), and (B,C) logistic growth with 20-year time delay and stochastic effect as dictated by Model 3B. The carrying capacity ( $K$ ) without snow was set at 400 caribou in all cases.

static, but fluctuates on a year-to-year basis and with greater amplitudes at high caribou densities.

The combination of stochasticity, logistic growth, and time-delay (Model 4) suggests practical difficulties involved with attempts to unmask the factors regulating or limiting caribou populations. Similarly, Hassell (1985) remarked on such stochastic obstacles in the use of  $k$ -factor analysis of the mechanisms of population regulation in invertebrates. Nonetheless, environmental noise remains the essence of the demography of numerous natural populations

(Strong 1986). We believe that a better theoretical and empirical understanding of these influences remains integral to the management of *Rangifer*.

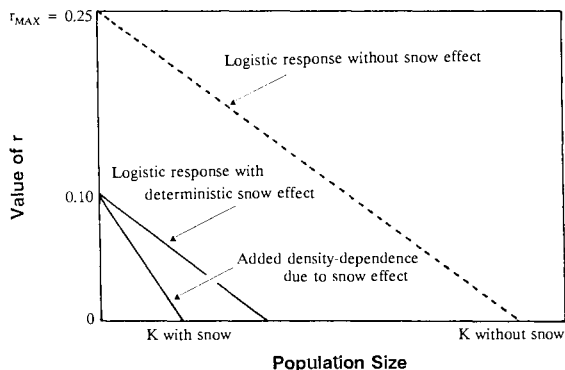


Figure 8. Hypothesised effects of snow on the rate of increase of caribou populations. (See text for explanation).

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