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Modeling density dependence and climatic disturbances in caribou: a case study from the Bathurst Island complex, Canadian High Arctic

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climate change; density independence; environmental stochasticity; Peary caribou; population dynamics; population viability analysis; simulation model.

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Abstract

Peary caribou *Rangifer tarandus pearyi* is the northernmost subspecies of *Rangifer* in North America and endemic to the Canadian High Arctic. Because of severe population declines following years of unfavorable winter weather with ice coating on the ground or thicker snow cover, it is believed that density-independent disturbance events are the primary driver for Peary caribou population dynamics. However, it is unclear to what extent density dependence may affect population dynamics of this species. Here, we test for different levels of density dependence in a stochastic, single-stage population model, based on available empirical information for the Bathurst Island complex (BIC) population in the Canadian High Arctic. We compare predicted densities with observed densities during 1961–2001 under various assumptions of the strength of density dependence. On the basis of our model, we found that scenarios with no or very low density dependence led to population densities far above observed densities. For average observed disturbance regimes, a carrying capacity of 0.1 caribou km^{-2} generated an average caribou density similar to that estimated for the BIC population over the past four decades. With our model we also tested the potential effects of climate change-related increases in the probability and severity of disturbance years, that is unusually poor winter conditions. On the basis of our simulation results, we found that, in particular, potential increases in disturbance severity (as opposed to disturbance frequency) may pose a considerable threat to the persistence of this species.

Introduction

Density dependence is a crucial component in the population dynamics of several species of ungulates (e.g. Messier *et al.*, 1988; Mduma, Sinclair & Hilborn, 1999; Kjellander *et al.*, 2004). Density dependence occurs when the growth rate of a population decreases as its density increases. Proximal ecological factors (e.g. declining forage resources with increasing population densities) may cause population growth rates to decrease through ultimate population factors (e.g. decreasing survival and/or reproduction). This mechanism could lead either to gradual reductions in population growth (Patterson & Power, 2002) or to abrupt population declines when resource overexploitation surpasses a critical level for maintenance of the population (Ferguson & Messier, 2000). In contrast, the timing of external disturbances is independent of the population density. Such density-independent events may lead to abrupt population declines when a population experiences particularly unfavorable environmental conditions (e.g. Miller, Russell & Gunn, 1977).

Density-dependent and density-independent mechanisms play important roles in the population dynamics of caribou and reindeer *Rangifer tarandus* (Solberg *et al.*, 2001). We use two terms to discuss the complex relationships that *Rangifer* have with their winter forage resources: availability and accessibility. First, *availability* of forage reflects the inherent ability of a given physical and climatic environment to produce vegetation that *Rangifer* may utilize to meet their energetic and other nutritional requirements. Second, *accessibility* of available winter forage is determined by snow-cover patterns. Physiographic patterns of terrain ruggedness, prevailing winds and snowfall produce prevailing snow-cover conditions, leading to spatial patterns of accessibility relative to available forage that are relatively consistent across a population's winter range from year to year (Nellemann, 1997).

As the density of *Rangifer* increases, the quantity and quality of digestible available forage on accessible sites may decline, that is the animals would have density-dependent impacts on forage resources where it is accessible in most years. However, the biomass of available and usually

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accessible forage, especially lichen, can accumulate during years or decades when *Rangifer* is absent, or during years when animal density is low enough, such that total annual primary production on accessible winter forage sites across the population's winter range is greater than the forage consumed or destroyed by trampling (e.g. Ferguson & Messier, 2000; Ferguson, Gauthier & Messier, 2001).

In some winters, snow-cover conditions may deviate greatly from that in most winters (e.g. extremely low or high snowfall, unusual amounts of ice formation or unusual winds during snow-cover accumulation). Such unusual conditions are expected to have density-independent effects on forage accessibility, not availability; the forage is still present, but it becomes less accessible. In winters with severe snow-cover conditions, increased forage inaccessibility may cause abruptly increased mortality, increased emigration, or subsequent reductions in recruitment and productivity. Such density-independent effects of forage inaccessibility on population dynamics may mask the detection of density-dependent impacts of *Rangifer* on their available forage, which may be the overriding factor that makes a population susceptible to density-independent factors (Reimers, 1983; Tyler, 1987; Adamczewski *et al*., 1988).

Peary caribou *Rangifer tarandus pearyi* is the northernmost subspecies of *Rangifer* in North America and endemic to the Canadian High Arctic (Banfield, 1961). During winter, Peary caribou search for forage on ridges or other topographical exposures where snow is absent, shallow or relatively soft (Larter & Nagy, 2001). Peary caribou forage includes gramminoids, forbs and dwarf shrubs (Shank, Wilkinson & Penner, 1978; Thomas & Edmonds, 1983), with a preference for patches with shallow or no snow where fruticose lichens and *Luzula* spp. occur (Thomas, Edmonds & Armbruster, 1999). Because of drastic population declines since 1961, the Government of Canada currently considers listing Peary caribou as endangered under the federal Species at Risk Act, as recommended by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2004).

Miller *et al*. (1977), Miller (1991, 1998), Gunn & Dragon (2002) and Miller & Gunn (2003*a*,*b*) have suggested that the population declines of Peary caribou have been triggered by density-independent climatic events. In particular, unusual weather in autumn or winter, resulting in ice coating on the ground or thicker snow cover, may make forage temporarily inaccessible. However, it is unclear whether or not and to what extent density dependence may contribute to the population dynamics of this species. For the purpose of this study, we therefore develop several scenarios of density dependence, based on a stochastic, single-stage population model parameterized with known historical densities, disturbance frequencies and effects of severe winters. We then compare the predicted densities to observed densities under various assumptions of the strength of density dependence.

Elucidating the roles of density dependence and climatic disturbances in the population dynamics of endangered Peary caribou is particularly important. Estimates of future population trends depend on realistic assumptions about the causative factors and ecological processes affecting this species; in turn, understanding the relative roles of such intertwined factors and processes is needed in order to conserve Peary caribou populations adequately, including sustainable harvests of local Inuit communities which depend on these animals for nutritional and cultural needs. Moreover, concerns have been raised about the potential impacts and persistence of Peary caribou, if the frequency and severity of winters increase with future climate change (Miller & Gunn, 2003*a*,*b*). To investigate these concerns, we also tested for a potential increase in the frequency and severity of disturbance events above known historical levels.

Methods

Habitat structure and population densities

The range of Peary caribou is large ($>800\,000\,km^2$), stable and relatively unaffected by human activity (COSEWIC, 2004). Peary caribou occur in six populations in the Canadian High Arctic: eastern Queen Elizabeth Islands, western Queen Elizabeth Islands, Banks Island and north-western Victoria Island, Prince of Wales Island and Sommerset Island, and Bathurst Island complex (BIC; Fig. 1); both Peary caribou and barren-ground caribou *Rangifer tarandus groenlandicus* occur on Boothia Peninsula. Traditional ecological knowledge (A. Taylor, unpubl. data) and scientific knowledge (Miller *et al*., 1977; Miller, 1998; Gunn & Dragon, 2002) suggest that some of these populations are connected by occasional emigration–immigration events across the sea ice. However, detailed knowledge about the frequency and magnitude of such events is not yet available. Less than 5% of the total range is vegetated (Gould, Raynolds & Walker, 2003), and only a fraction of vegetated areas are accessible to Peary caribou from mid- to late winter (i.e. usually November–May). Plant productivity is

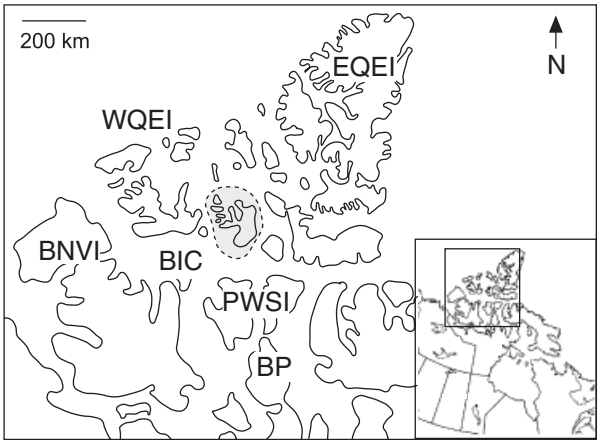

Figure 1 Locations of Peary caribou *Rangifer tarandus pearyi* populations in the Canadian High Arctic: Eastern Queen Elizabeth Islands (EQEI), western Queen Elizabeth Islands (WQEI), Banks Island and north-western Victoria Island (BNVI), Prince of Wales Island and Sommerset Island (PWSI), Boothia Peninsula (BP) and Bathurst Island complex (BIC, shaded area).

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Table 1 Population abundance, density and annual growth rates for Peary caribou *Rangifer tarandus pearyi* for the Bathurst Island complex (BIC) for 1961–2001

Year of survey	Abundance	Density (km^2)	Reference	Annual growth rate
1961	3608	0.186	Tener (1963)	
1973	897	0.046	Miller (1998)	0.890
1974	**266**	**0.013**	**Miller *et al.* (1977)**	**0.297**
1985	727	0.037	Miller (1987)	1.096
1988	1103	0.057	Miller (1989)	1.149
1993	2387	0.123	Miller (1995)	1.167
1994	3011	0.155	Miller (1998)	1.262
1995	**2200**	**0.113**	**Miller (1998)**	**0.731**
1996	**552**	**0.028**	**Miller (1998)**	**0.251**
1997	**78**	**0.004**	**Gunn & Dragon (2002)**	**0.141**
2001	240	0.012	M. A. D. Ferguson (unpubl. data)	1.324

The total area of BIC is *c.* 19 436 km^2. The highlighted years (in bold) indicate die-off years.

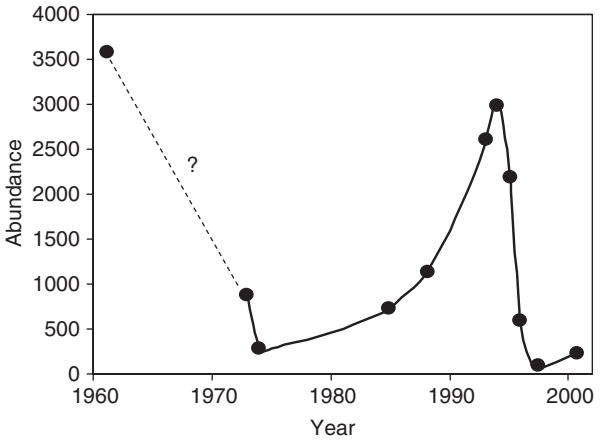

Figure 2 Estimated Peary caribou *Rangifer tarandus pearyi* abundance for the Bathurst Island complex (BIC) for 1961–2001. The solid line indicates the estimated population trend based on 11 survey years (see Table 1).

very low with above- and belowground net primary productivity of less than 20 g m^{-2} year^{-1} and overall aboveground plant biomass of less than 100 g m^{-2} (Gould *et al.*, 2003).

The best time series of estimates of population abundance exists for the population occupying the BIC with 11 survey years since 1961 including knowledge of years with population crashes that occurred during severe winters (Table 1 and Fig. 2). The BIC population declined from about 3600 Peary caribou in 1961 to almost 300 in 1974, increased to more than 3000 by 1994, and then crashed to less than 100 in 1997 after three severe winters. On the basis of a polynomial fit derived from those survey years (Fig. 2), the estimated average density for BIC during 1961–2001 was 0.054 caribou km^{-2} over a total area of 19 400 km^2. For the other populations, densities ranged between 0.013 and 0.171 animals km^{-2} on Banks Island and north-western Victoria Island, 0.017 and 0.149 on Boothia Peninsula, 0.012 and 0.268 on western Queen Elizabeth Islands, and 0.001 and 0.101 on Prince of Wales Island and Sommerset Island (see COSEWIC, 2004). The eastern Queen Elizabeth Islands have never been adequately surveyed, although Tener (1963) suggested that about 1500 Peary caribou occurred there in 1961.

Modeling approach

We used Ramas® Metapop 4.0 (Akçakaya & Root, 2002) to develop a stochastic, single-stage population model for the BIC population. Ramas® Metapop has been used in many studies of population viability and habitat suitability (e.g. Akçakaya & Raphael, 1998; Schtickzelle & Baguette, 2004). We chose to parameterize an existing software package as it allows transparency and simplicity. For the aim of this study we applied a one-stage model; that is simulations are based on adult caribou only. While a multi-stage matrix model assumes different fecundity rates and transition probabilities of survival between different life-history stages, a one-stage model has a single expected growth rate (R) for the population or sub-population. Moreover, Peary caribou reproduction is extremely variable (Larter & Nagy, 2000) and empirical data on mortality rates at different ages are scarce. In the model we did not consider dispersal, that is we assumed that the net sum of immigration versus emigration between BIC and adjacent populations such as the western Queen Elizabeth Islands, eastern Queen Elizabeth Islands, or Prince of Wales Island and Sommerset Island equaled zero.

Growth rate and density dependence

Assuming that food resources are shared equally among individuals (i.e. scramble competition), forage availability per individual would decrease as population density increases, when and if annual forage loss due to grazing exceeds annual production. In the model, annual growth of a population is a function of its density in the previous year under the assumption of scramble competition:

$$R_t = R_{\max} e^{\frac{-\ln R_{\max} N_{t-1}}{K}} \quad (1)$$

with t as the annual time step, R_t as growth rate, N_t as population size, R_{max} as maximum growth rate (at $N_{t-1} = 0$) and K as carrying capacity. R_{max} is the maximum annual growth rate at which the population may increase in the absence of density dependence. In the model, we applied a maximum annual increase of 22% based on the average annual growth rates for BIC between the survey years of 1985, 1988, 1993 and 1994 and between 1997 and 2001 (Table 1). This value seems to be a realistic assumption as it is less than the theoretical finite rate of increase (λ) of 1.3 and the maximum rates realized by most introduced *Rangifer* populations (Bergerud, 1980; Heard, 1990), and above the overall 20-year value of 1.13 from 1974 to 1994 (Table 1 and Miller, 1998).

Carrying capacity

For scramble competition, the carrying capacity K is the population density at which $R_t = 1.0$. When population density exceeds K, the rate of population growth will become negative. Thus, if K is high, density dependence would cause a smooth decline in R as population density increases. However, if K is low, R would decrease more steeply. For the BIC population model, we tested K values in the range from 0.05 to 0.5 caribou km^{-2}, or from 27 to 270% of the maximum density estimated since 1961 (Table 1). Applying this range enables one to detect the level of density dependence that may be inherent to population dynamics of BIC Peary caribou. In the model, the initial value for K was kept constant, that is we assumed that the total amount of accessible forage did not change over time. This may be a pessimistic assumption for caribou population persistence under climate warming; however, we believe more empirical data are needed in order to include such multiple effects.

Climatic disturbance

On the basis of four severe winters that caused significant adult mortality in the BIC during 1961–2001 (Table 1 and Miller & Gunn, 2003*a*,*b*), we estimated $P_{disturbance}$, the annual probability of disturbance, to be 0.1 (Table 2). If an event strikes a local population at a certain time, a given proportion of adults is removed from the population. We estimated the mean adult die-off at 60%, based on reported population declines for the BCI population following years of severe winter conditions (Miller & Gunn, 2003*a*,*b*). To introduce a stochastic range of mortality, the magnitude of any particular disturbance event is randomly selected between 50 and 70% (Table 2). These parameters allowed us to introduce the effects of unusual winters in which accessibility of winter forage was drastically reduced by severe snow/ice cover.

Demographic and environmental stochasticity

We implemented demographic stochasticity by sampling the number of survivors from binomial distributions and the number of young from a Poisson distribution. Because of the lack of empirical data, we used a wide range of population viability studies (Akçakaya *et al.*, 2004) to find a realistic degree of environmental stochasticity. In the BIC population model, environmental stochasticity that was unrelated to the highly reduced accessibility of winter forage was incorporated by sampling random numbers for R_t from a lognormal distribution with an estimated coefficient of variation (CV) of 0.1 (CV_{R_t}; Table 2) and a CV for the carrying capacity of 0.2 (CV_K; Table 2). Such annual fluctuations in the carrying capacity represent natural variation in the availability of winter forage and quality of summer forage.

Table 2 Parameters and variables used in the Bathurst Island complex (BIC) Peary caribou *Rangifer tarandus pearyi* simulation model

Parameter/ variable	Description	Value
$D_{observed}$	Average observed population density 1961–2001 (caribou km^{-2})	0.054
D_{init}	Initial population density (caribou km^{-2})	0.054
K	Carrying capacity (caribou km^{-2})	0.05–0.5*
CV_K	Coefficient of variation of carrying capacity	0.2
R_{max}	Maximum growth rate	1.22
CV_{R_t}	Coefficient of variation of annual growth rate	0.1
$P_{disturbance}$	Annual probability of disturbance	0.1
$Prop_{die\text{-}off}$	Proportion of die-off following disturbance	50–70%
t	Simulation time (years)	100

Parameter values with an asterisk indicate the range of variation under different model assumptions.

Simulation scenarios

For the aim of this study, we looked for a realistic level of density dependence for which the average predicted caribou density of the BIC population model was similar to the average observed caribou density over the past 40 years. Therefore, for each density dependence scenario we ran 1000 iterations on the base of time step $t = 1$ year for 100 years with the initial population size being equivalent to the average observed caribou density. To test for different levels of density dependence, we varied the carrying capacity K in the range of 0.05–0.5 caribou km^{-2} (Table 2). As future changes in the disturbance regime related to climate change may have profound effects on the population dynamics of Peary caribou, we also tested for variations in the severity of density-independent climatic disturbances by varying the probability of disturbance, $P_{disturbance}$, and the proportions of caribou dying off following a disturbance, $Prop_{die\text{-}off}$.

Results

On the basis of our simulation results we found that the population dynamics of Peary caribou are driven by both density-dependent and density-independent mechanisms.

Even though density-independent die-off events during 'poor' winters significantly shaped the temporal pattern of population dynamics (Fig. 3), density dependence plays an important role in 'normal' winters: very low density dependence led to average population densities far above densities observed during the past four decades (Fig. 4). For example, a K value of 0.4 caribou km^{-2} resulted in an average density of 0.22 caribou km^{-2}, a value higher than any maximum density observed during 1961–2001. We also implemented simulation scenarios with no density dependence (mortality is then only driven by die-off in disturbance winters). For this scenario and a disturbance probability of 0.1 with an average die-off of 60%, average population densities reached more than 1.0 caribou km^{-2} (not shown). Assuming a disturbance probability of 0.1 (i.e. an average frequency of once every 10 years) and an average die-off of 60% (equivalent to the average disturbance regime for 1961–2001), a carrying capacity of 0.1 caribou km^{-2} generated the same average density as experienced by the BIC population over the past four decades. Carrying capacities below this value (i.e. very high density dependence) yielded population densities lower than observed densities. On the basis of the model assumptions for the BIC population model, our results indicated that the predicted density of caribou was 56.4% of the implemented carrying capacity.

Assuming a carrying capacity of 0.1 caribou km^{-2}, the probability of extinction for the BIC population within a time frame of 100 years was estimated to be near zero under the current regime of climatic events, where 50–70% of adults died when the average disturbance frequency was 10 years. However, as future climate change may affect the severity and frequency of density-independent disturbance events, we also analyzed the effects of variations in the disturbance regime on average densities and the risk of extinction (Fig. 5). For example, a 50% increase in the probability of annual disturbance to 0.15 resulted in an average density of 0.0327 caribou km^{-2} with an extinction risk of 5.5%. Increases in both frequency and severity to 50% (i.e. 0.15 annual disturbance probability and 90% proportion of die-off) had synergistic effects with an extinction risk of 96.6% and an average density of 0.001 caribou km^{-2}. A 50% increase in the proportion of die-off alone resulted in an extinction risk of 73.8% and an average density of 0.0084 caribou km^{-2}. For a proportionally equal increase in both parameters, these results therefore indicate that disturbance severity has a larger impact than disturbance frequency.

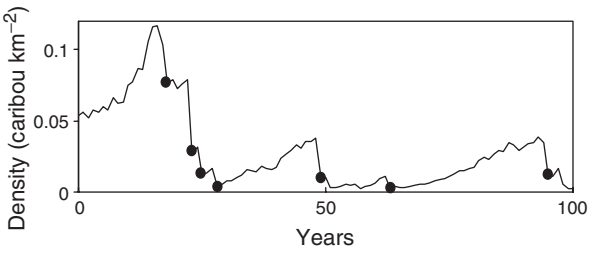

Figure 3 Typical simulation run for the Bathurst Island complex (BIC) Peary caribou *Rangifer tarandus pearyi* population with a carrying capacity of $K = 0.1$ caribou km^{-2}. The black dots indicate population crashes following climatic disturbance events.

Discussion

On the basis of our BIC population model, we conclude that density dependence may be a crucial component in the population dynamics of High Arctic Peary caribou. Model scenarios with average disturbance regimes for 1961–2001 and very low or no density dependence led to significantly higher caribou densities than those observed during this period (Fig. 4). For a carrying capacity of 0.1 caribou km^{-2}, the model generated densities similar to those observed during the past four decades. This contradicts the prevailing belief that population dynamics of Peary caribou are largely governed by extrinsic, environmental disturbances (e.g. Miller, 1998). For example, before the die-off in 1994, Miller & Gunn (2003*a*,*b*) found relatively high production and calf survival and therefore concluded that density dependence was not likely to be in effect. We acknowledge that density-independent climatic disturbances may regulate stochastic die-off events when winter conditions are extremely poor and forage accessibility is severely reduced. However, as opposed to the findings of Miller & Gunn (2003*a*,*b*) we suggest that in 'normal' years annual population growth may be subject to density dependence. This is also supported by traditional ecological knowledge: in the early 1990s during a period of increase, Inuit in Resolute Bay predicted that the population on BIC would decline during the next severe winter because they believed that there were too many

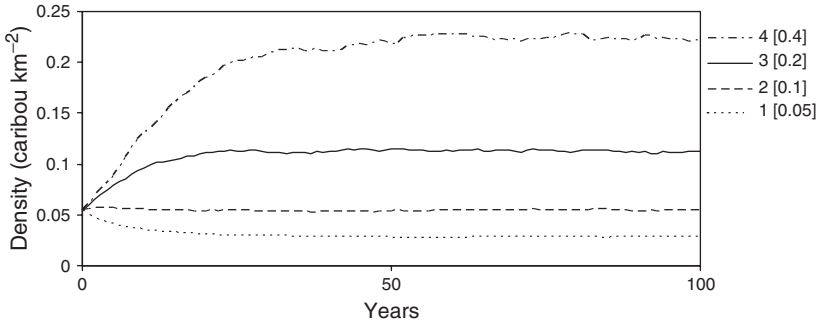

Figure 4 Mean population trajectory for the Bathurst Island complex (BIC) population for 1000 replicate simulation runs under four different density dependence scenarios (with K value given in caribou km^{-2} in parentheses, respectively). The initial BIC population density of 0.054 caribou km^{-2} at $t = 0$ is based on average observed densities for 1961–2001.

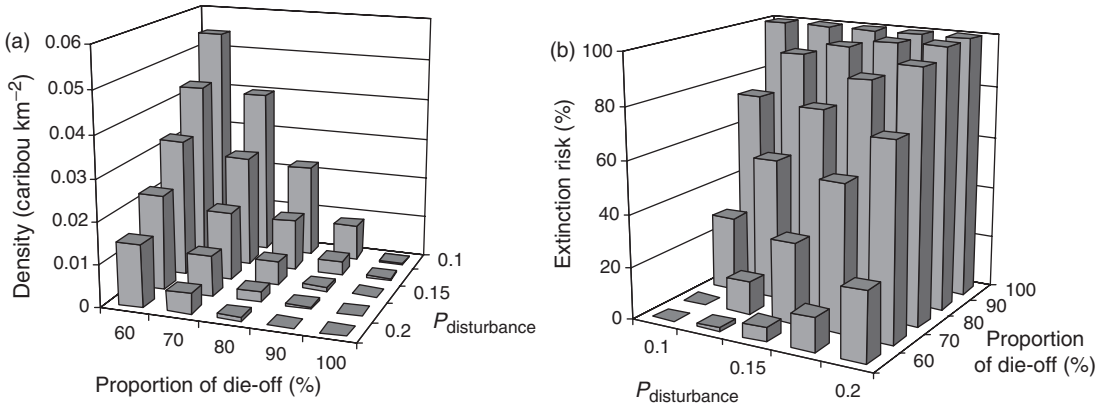

Figure 5 Mean Peary caribou *Rangifer tarandus pearyi* density for the Bathurst Island complex (a) and extinction risk after 100 years (b) for varying scenarios of $P_{disturbance}$ and proportions of die-off following a disturbance event. The carrying capacity was fixed at 0.1 caribou km^{-2}.

caribou. Although not directly shown in this study, we hypothesize that density dependence and density independence may affect population dynamics in both 'poor' and 'normal' years. In 'normal' years population growth may be affected by climatic variables (altering forage accessibility and quality) as well as population density (altering forage availability). In 'poor' winters (i.e. disturbance years) climate is the primary driver for die-off severity. However, the actual population density in such disturbance years may regulate the die-off severity too. For example, under low population densities, inaccessibility of forage may result in a proportionally lower die-off as opposed to a situation where forage inaccessibility strikes a population at high densities. In other words, a smaller population may still be able to utilize the sparsely distributed resources during a disturbance winter. This view is furthermore supported by traditional knowledge of some Inuit in Resolute Bay (M. A. D. Ferguson, pers. comm.). Considering density-dependent mechanisms in population growth is therefore important, even when mortality events caused by unusually severe winter conditions may be a dominant factor in the population dynamics of this species.

On the basis of available aboveground biomass and daily diet requirements of Peary caribou, Miller (1998) calculated that even at maximum historic BIC caribou densities only 2% of the total available forage would be required to maintain viable populations (and therefore density dependence may not apply to Peary caribou). However, it is known that Peary caribou are associated with particular habitats, especially in winter (e.g. topographical exposures, shallow-covered ridges with *Luzula* spp. and lichens; Thomas & Edmonds, 1983; Thomas *et al.*, 1999). In winter Peary caribou avoid habitats with deep snow, as found in valley bottoms and on the lower levels of slopes in rugged uplands where vegetation is usually more abundant and lush. They also avoid flat terrain and windward slopes where snow may be relatively thin but too hard for foraging. In addition, Peary caribou are selective grazers, utilizing a small proportion of available vegetation, even in summer. As a consequence, accessible forage biomass, even in normal winters, is significantly less than the total amount of available plant biomass. The effective densities of Peary caribou on portions of their winter range where forage is accessible are probably many orders of magnitude greater than is apparent, and therefore density-dependent mechanisms could affect Peary caribou population dynamics. This conclusion is supported by the results of our model, which indicated that with extremely low or no density dependence, population densities would tend to be much higher than any maximum historic density for the BIC during 1961–2001.

Even though several climatic shifts have occurred in the circumpolar Arctic during past millennia and caribou were capable of adapting to it (Ferguson, 1996), it has been hypothesized that recent and future anthropogenic climate change may pose a major threat to Peary caribou (Gunn, 1998; Miller & Gunn, 2003*a*,*b*). Our BIC model generally supports the hypothesis that an increase in the frequency and severity of unusually poor winter conditions may have a significant impact on the persistence of this species. In particular, a potential increase in the proportion of die-off (i.e. disturbance severity) may pose a higher threat than similar proportional changes in the frequency of climatic disturbances. This might be due to the fact that Peary caribou are generally able to recover relatively quickly following a disturbance winter. On the other hand, Peary caribou may also benefit from greater plant growth as a result of warmer summer temperatures and increased moisture from melting snow cover. If climate change effects on improved primary productivity are weak, warmer winter weather may increase the frequency of rain on snow (i.e. icing) events, resulting in long-term decrease of population densities.

Evaluation of both density-dependent processes and the potential impacts of climate change should be a major conservation priority for Peary caribou. Detailed analysis of weather variables is a difficult if not impossible task. Even if meteorological stations were more common in the High Arctic, parameters measured at such stations cannot describe the spatial and temporal patterns of snow cover as it may affect the accessibility of forage within the vast range

occupied by Peary caribou. Also, the availability of forage to Peary caribou should be monitored within sites where it is usually accessible to these selective grazers. In the future, the availability and productivity of vegetation across the High Arctic could mask significant changes in the quantity and quality of winter forage accessible to these animals. Our model results are an initial step to assess the potential negative consequences of climate change on Peary caribou.

Improved understanding of both density-dependent and density-independent processes and the population dynamics of Peary caribou are important to the Inuit in High Arctic communities, because animals form a central part of Inuit culture and diet. The Inuit of Resolute Bay have carefully monitored and restricted their harvest of Peary caribou in the BIC since at least 1975 through self-imposed regulations. In the future, harvesting must be balanced against the risks of density-independent weather-mediated declines. The actions of Inuit since 1975 suggest that they could implement such a balance, especially if strengthened by a better understanding of the population's winter ecology.

Model limitations and uncertainty

Because of information gaps about the biology and population dynamics of Peary caribou, and the resulting simplified one-stage model, our results are subject to an unknown degree of uncertainty. For example, if actual population densities for 1961–2001 were higher than estimated (e.g. missing survey years may have had higher abundances than surveyed years, or surveys may have underestimated actual populations to differing degrees), this would imply a higher carrying capacity than estimated (i.e. density dependence would have been lower). A lower density dependence effect may also result from the effects of temporal autocorrelation of disturbance events: under high temporal autocorrelation one would expect a proportionally higher impact of climatic disturbances and therefore a higher carrying capacity in order to generate the same average population density.

Our model was inherently conservative or pessimistic because we did not incorporate the potential positive effects of unusually mild winters on population productivity and survival. Also, we did not incorporate the potential benefits that climate change could have on earlier snowmelt, later snow accumulation and vegetation growth. Thus, we view our results as indicative of worst-case scenarios. Further data on potential changes in primary productivity and climate are needed for such analysis.

Final conclusions

Our model results suggest the importance of assessing density-dependent mechanisms in understanding the population dynamics and ecology of endangered Peary caribou. The inaccessibility of a large proportion of the vegetation due to extensively hard snow cover in most winters may explain why density-dependent mechanisms are in effect, even at relatively low population densities. However, despite the underlying importance of density-dependent mechanisms, major changes in population dynamics of the Peary caribou may be driven by external, environmental perturbations (i.e. winter climatic events). If the frequency and intensity of such events increase in the coming decades, this may lead to an increased risk of extinction for some populations of this species. To better predict the fate of the Peary caribou, more demographic and environmental data are needed, especially on interannual landscape scale variability in the accessibility of forage and the ability of Peary caribou to adapt to potential interannual changes in spatial patterns of winter forage accessibility. Ongoing and future research on scientific and traditional ecological knowledge may provide such information, allowing improvements in the definition of population modeling parameters.

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