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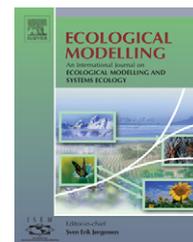
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Potential net effects of climate change on High Arctic Peary caribou: Lessons from a spatially explicit simulation model

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ABSTRACT

It is anticipated that climate change will have a major impact on High Arctic ecosystems. Peary caribou (*Rangifer tarandus pearyi*) is a caribou subspecies endemic to the Canadian High Arctic. In the past four decades, population dynamics of Peary caribou have been subject to several population die-offs due to unfavorable winter weather with ice coating on the ground or thicker-than-usual snow cover. There is general consensus that such disturbance years may increase in frequency and severity as a result of climate change. However, there is also evidence that available forage may increase due to a longer and warmer growing season. In this study we assess the net effects of climate change with a spatially explicit simulation model calibrated with data from the Bathurst Island complex (BIC) in the Canadian High Arctic. In particular, we ask under which climate change scenarios populations depart from the current conditions and either suffer or benefit from changes in the climate. The model incorporates movement of caribou groups and annual primary productivity over 100 years. Based on the model we suggest that Peary caribou may experience significantly lower population die-offs during disturbance years if biomass increases by 50% as projected within the next 100 years and if the currently estimated proportion of inaccessible caribou forage during such disturbance events does not change with climate change. However, if forage inaccessibility in poor winters increases by more than 30% over the next 100 years, caribou may experience negative net effects of climate change. This is the first comprehensive modeling study on this species and therefore of particular importance for wildlife management and local Inuit who rely on caribou as part of their culture, identity, and diet.

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1. Introduction

Global climate change has been recognized as a major threat for the persistence of species and the integrity of ecosystems (e.g., Pounds et al., 2006). The scientific community

has tried to provide policymakers with sound projections of species responses to climate change. For example, recent empirical distribution models (also coined climate-envelope models) have been used to make predictions about the fate of biodiversity under climate change (e.g., Thomas et

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al., 2004). However, researchers remain uncertain about the feasibility of such methodologies and they debate the validity of predictions (Buckley and Roughgarden, 2004; Thuiller et al., 2004; Harte et al., 2004). Such multi-species models may be a powerful tool to draw the attention of policymakers; however, they are subject to a high degree of uncertainty.

Mechanistic, bottom-up simulation models provide a useful alternative, as they can be tailored towards simulating direct changes in species' vital rates and indirect effects through consumer–resource interactions (Grimm and Railsback, 2005). The bottom-up strategy of such models is to compile relevant information about entities at a lower level of the system (i.e., individuals), formulate theories about their behavior, incorporate these theoretical behaviors into a simulation model, and observe the emergence of system-level properties related to particular questions (Grimm et al., 2005). As climate change has direct effects on the population and/or individual level and is often related to stochastic events (e.g., precipitation, disturbances), stochastic simulation models have been touted as a promising tool for bottom-up studies of environmental change (Tews, in press).

On the species level both positive and negative effects may result from climate change (Hulme, 2005). Climate change effects can also change over time depending on the environmental conditions. Overall, there is large uncertainty about the magnitude and direction of climatic changes and how these changes directly or indirectly translate to positive and/or negative effects for species (ACIA, 2005). A majority of empirical studies have found negative effects (Wichmann, 2005). However, studies with no clear trend of climate change implications did not consider under which conditions net effects may shift from positive to negative (or vice versa). In this study we ask: under which future climatic conditions does a species depart (either positively or negatively) from its current status? We believe that assessing such thresholds and patterns is a crucial task in understanding the uncertainty of climate change implications.

In this paper we present a case study on High Arctic Peary caribou (*Rangifer tarandus pearyi*), an endemic caribou subspecies in Canada's Arctic that has been recommended for listing as endangered (COSEWIC, 2004). In this region changes in the earth's climate are projected to be particularly intense (ACIA, 2005). During the past few decades Peary caribou have experienced irregular population declines as a result of climatic disturbance events (Miller et al., 1977; Miller, 1991; Gunn and Dragon, 2002; Miller and Gunn, 2003; Tews et al., 2007). In such years, unusual winter weather with ice coating the tundra vegetation and thicker-than-usual snow cover may result in temporarily inaccessible forage, leading to malnutrition and starvation. Over the past four decades, Peary caribou on the Bathurst Island complex (BIC) have experienced four extreme winters with significant population die-offs (Miller and Gunn, 2003). It is anticipated that both the frequency and the severity of such climatic events may increase under climate change (ACIA, 2005).

On the other hand, climate change may result in a longer growing season and increased primary productivity (ACIA, 2005), which could provide additional caribou forage in the otherwise sparsely vegetated polar desert. Epstein et al. (2000)

developed a vegetation simulation model and predicted about a 50% increase in aboveground biomass for the High Arctic over the next 100 years. If biomass becomes more available, but winter disturbance events also become more frequent and severe, how may the population dynamics of Peary caribou respond? Under which assumptions of climate change are Peary caribou predicted to experience net positive versus negative effects of climate change? To address these questions, we developed a spatial simulation model based on the BIC population in the Canadian High Arctic. The analysis of potential climate change effects on Peary caribou are of high priority both for wildlife management and local Inuit who, despite lifestyle changes, continue to rely on caribou as an important part of their culture, identity, and diet. In addition, our study also provides a case study of multiple, counteracting effects of climate change.

2. Methods

2.1. Species and habitat

Peary caribou is an endemic caribou subspecies occurring in six populations across the Canadian High Arctic: eastern Queen Elizabeth Islands, western Queen Elizabeth Islands, Banks Island and northwestern Victoria Island, Prince of Wales Island and Sommerset Island, and the Bathurst Island complex (COSEWIC, 2004). Overall Peary caribou occur in low densities within a large range of more than 800,000 km². During the last few decades total population estimates for the Canadian High Arctic were generally below 30,000 animals (COSEWIC, 2004). Less than 5% of the total range is vegetated, and only a fraction of the vegetated areas are accessible to Peary caribou during the winter (October–May). For Peary caribou to survive the winter, their winter forage must be both available and accessible. Availability of forage reflects the ability of the environment to produce vegetation that caribou may use to meet their energetic and nutritional requirements. Accessibility of available winter forage is determined by terrain ruggedness, prevailing winds and form of precipitation (e.g., snow, or rain on snow turning to ice). The spatial pattern of accessibility relative to available forage is relatively consistent across a population's winter range from year to year (Nellemann, 1997).

During winter, Peary caribou search for forage mainly on ridges and well-drained uplands that are among the least productive vegetated areas (Larter and Nagy, 2001). However, in these areas snow is either absent, shallow or relatively soft which makes forage relatively accessible for Peary caribou. In the High Arctic plant productivity is very low, with aboveground biomass of less than 100 gm⁻² in most areas (Gould et al., 2003). One of the most surveyed populations in the Canadian High Arctic is the BIC population with eleven survey years since 1961 and four reported die-offs during severe winters (i.e., 1973/1974, 1994/1995, 1995/1996, 1996/1997). The BIC population declined from about 3600 Peary caribou in 1961 to about 750 in 1973, but crashed to almost 300 in 1974 (Miller et al., 1977). Subsequently, the population recovered to more than 3000 by 1994, and then crashed to fewer than 100 in 1997 after three severe winters.

2.2. General model description

Peary Caribou Simulation Model (PCSimMod) is a grid-based simulation tool to study the impact of climate change on Peary caribou population dynamics in the Canadian High Arctic. Groups of caribou move across a simulated landscape with a daily time step; the model runs for 100 simulated years. The model incorporates annual net primary productivity, i.e., the vegetation reproduces each year depending on the annual climate. Population die-off is modeled spatially explicit on a daily basis, i.e., individuals will start to die if their physical status declines to a certain level. This may happen during poor winters when a large proportion of the sparsely distributed forage becomes temporarily inaccessible. Whereas disturbance-related mortality is spatially explicit and individual-based on a daily time step, population-based fecundity and mortality is applied to the entire population once a year, based on a scramble competition density-dependent function.

To compare differences among climate change scenarios, the model calculates relative changes in the expected minimum abundance (EMA), a common measure in population viability analysis (McCarthy and Thompson, 2001). The EMA measures the lowest abundance during a single 100-year simulation run, averaged over all replicates. If not mentioned otherwise, each simulation run was replicated 100 times.

The model cell size of 4 km² equals the average daily movement range reported for other sedentary arctic caribou (Bergman et al., 2000). The parameter calibration of PCSimMod is based on empirical data from the Bathurst Island complex population. The model's spatial extent of 70 cells × 70 cells equals the approximate size of the BIC area. Based on average estimated abundances for the BIC population (see Table 1), the initial population size, $Abundance_{init}$ in each simulation run is 1047. The initial number of caribou is randomly distributed across the grid on the first day in the first year of a simulation run.

As described above, PCSimMod is based on two major components: annual population growth and individual-based disturbance mortality (Figs. 1 and 2). Annual population growth is based on the maximum growth rate, population size and carrying capacity, the latter being a function of available and accessible forage, annual net primary productivity (ANPP) of aboveground biomass, and forage consumption by caribou. Individual-based disturbance mortality represents the die-off severity during winter when caribou move across the landscape, are unable to access sufficient forage, become malnourished and die because of poor physical condition.

2.3. Population growth

Annual population growth rate is modeled as scramble competition, under the assumption that population growth rate decreases as population size increases:

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

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

in the absence of density dependence. In the model, we used $R_{max} = 1.22$ (i.e., a maximum annual increase of 22%) based on annual growth rates for BIC between the survey years of 1985, 1988, 1993, and 1994 and between 1997 and 2001 (Miller, 1987, 1989, 1995, 1998; Gunn and Dragon, 2002; Ferguson, unpublished data). To incorporate environmental stochasticity, we estimated a coefficient of variation of 10% for the maximum growth rate applied each year (Table 1). On June 1st in each simulation year, the model calculates the annual population growth rate and individual caribou are subtracted or added to the current population in randomly selected occupied cells.

2.4. Carrying capacity

For scramble competition, the carrying capacity, K , is the population size at which $R_t = 1.0$, and above which the population growth rate is negative. Here we define K as the maximum population size that can be sustained by the annual net primary productivity of accessible biomass of the previous winter:

$$K = \frac{\sum_{i,j} A_{ct} \times v}{\sum_{i,j} Abundance \times F_{total}}, \quad (2)$$

where A_{ct} is the accessible biomass per cell, v the annual net primary productivity and F_{total} is the total amount of forage intake per caribou per year (Table 1). The denominator represents the total annual amount of forage required to sustain the current population. The carrying capacity was therefore calculated based on biomass annually accessible for the BIC population.

2.5. Aboveground forage biomass

Each cell in the model is assigned a maximum availability of forage per cell, $A_{v(max)(ij)}$. These values are randomly selected from the actual frequency distribution of biomass data for the BIC area inferred from published data (Table 2). For the simulated BIC area the average amount of available forage across all cells is 49.5 gm⁻², which is within the range reported for the High Arctic (Gould et al., 2003). At the beginning of a simulation run, each cell begins at its maximum value. Over the course of the simulation run, the actual amount of available biomass, $A_{v(t)}$, ranges between 0 and that cell's $A_{v(max)(ij)}$ value. In other words, $A_{v(max)(ij)}$ defines the upper limit of available biomass for each cell, whereas $A_{v(t)}$ keeps track of the actual amount of available biomass, which depends on the daily amount that is consumed by caribou and the amount annually re-growing. Generally, the proportion of the available forage that is accessible, $A_{c(t)}$, is high in areas with low biomass and low in high productivity sites. From June to September accessibility is unrestricted due to the lack of a snow cover. Each day for each cell $A_{c(t)}$ is calculated as

$$A_{c(t)(ij)} = A_{c(max)(ij)} - (A_{v(max)(ij)} - A_{v(t)(ij)}), \quad (3)$$

where $A_{v(max)(ij)} - A_{v(t)(ij)}$ represents the amount of forage consumed. The maximum amount accessible during winter,

Table 1 – Parameters and variables used for the standard scenario in the simulation model

Parameter/variable	Value/range	Description	Reference
Model structure			
t	t = 1 (360 days)	Time step	–
c	4 km ²	Cell size equals estimated daily moving range	Bergman et al. (2000)
G	19,600 km ²	Grid size equals size of Bathurst Island complex (BIC)	–
Abundance _(ij)	–	Number of caribou per cell	–
Abundance _{max.summer(ij)}	25	Maximum number of caribou per cell (summer)	Miller and Gunn (1982), Gunn and Dragon (2002)
Abundance _{max.winter(ij)}	15	Maximum number of caribou per cell (winter)	Miller and Gunn (1982), Gunn and Dragon (2002)
Abundance _{init}	1047	Initial number of caribou; average population size based on population trend 1985–2001	Miller (1987, 1989, 1995, 1998), Gunn and Dragon (2002), Ferguson (unpublished data)
Population growth			
R _t	–	Annual growth rate: $R_t = R_{max} e^{-(\ln R_{max} N_{t-1})/K}$	–
R _{max}	1.22	Maximum growth rate	Miller (1987, 1989, 1995, 1998), Gunn and Dragon (2002), Ferguson (unpublished data)
CV _{R,max}	0.1	Coefficient of variation of maximum growth rate	Own estimation
K	–	Carrying capacity, i.e., maximum abundance sustained by annual primary productivity of accessible forage: $K = \sum_{i,j} A_{ct} \times v / \sum_{i,j} Abundance \times F_{total}$	–
Aboveground biomass			
A _{v(max)(ij)}	0–500 g m ⁻²	Maximum available aboveground biomass per cell	Bliss and Matveyeva (1992), Gould et al. (2003), CAVM Team (2003)
A _{v(t)(ij)}	0–500 g m ⁻²	Available aboveground biomass per cell	–
f	0.265	Maximum proportion of available aboveground biomass accessible during winter	Own estimation
z	0–0.265	Proportion of available aboveground biomass accessible per cell: $z = f e^{-10(A_{v(max)(ij)}/A_{v(max)})}$	Own estimation
A _{c(max)(ij)}	A _{v(max)} × z	Maximum available aboveground biomass accessible per cell	–
A _{c(t)(ij)}	A _{c(max)} – (A _{v(max)} – A _{v(t)})	Available aboveground biomass accessible per cell	–
Annual net primary productivity (ANPP)			
g	0.0006	Annual net primary productivity (ANPP) factor	–
pb	0–0.3	P/B ratio; increases with biomass: $pb = g \times A_{v(t)}$	Gould et al. (2003)
CV _g	10%	Coefficient of variation of ANPP	Knapp and Smith (2001)
Forage consumption			
F _{winter}	1.5 kg/day	Amount of average daily winter forage intake (October–May)	Parker et al. (2005)
F _{summer}	2.5 kg/day	Amount of average daily summer forage intake (June–September)	Parker et al. (2005)
F _{total}	660 kg	Total amount of forage intake per year and caribou: $F_{winter} \times 240 \text{ days} + F_{summer} \times 120 \text{ days}$	–
Movement			
P _{random.walk}	0.5	Daily probability to move to a randomly chosen adjacent cell; P _{random.walk} = 1.0 if A _{c(t)(ij)} < Abundance _(ij) × F _{summer/winter}	Own estimation
Disturbance			
P _{disturbance}	0.1	Probability of disturbance	Miller and Gunn (2003)
S	0.0009	Proportion of accessible forage A _{c(t)} in disturbance winters (A _{c(t)} × S)	Own estimation
CV _S	0.25	Coefficient of variation of S, i.e., spatial variation in inaccessibility	Own estimation

Parameter/variable	Value/range	Description	Reference
L_{init}	14	Physical status in winter; 14 initial points are assigned for each individual; reduced by 1 point for each day where $A_{c(t)} < Abundance_{(ij)} \times F_{winter}$; accumulate 1 point to a maximum of $L = 14$ where $A_{c(t)} > Abundance_{(ij)} \times F_{winter}$; if $L = 0$ individuals die deterministically	Own estimation
Dispersal D	5%	Dispersal rate; annual percentage of carrying capacity subject to dispersal	Own estimation
$P_{emigration}$	0–1.0	Probability of emigration for D , increases linearly from 0 to 1.0 until carrying capacity is reached	–
$P_{immigration}$	0.18	Probability of immigration for D	–

$A_{c(max)(ij)}$, is defined as

$$A_{c(max)(ij)} = A_{v(max)(ij)} \times z, \tag{4}$$

with z calculated through the exponential function

$$z = f e^{-10(A_{v(max)(ij)} / A_{v(max)})}, \tag{5}$$

where f is the maximum proportion of available aboveground biomass accessible during winter and $A_{v(max)}$ is the maximum amount of available forage, i.e., 500 gm^{-2} . For the standard parameter set f was fixed at 0.265, i.e., 26.5% of aboveground biomass would be accessible for cells with biomass availability near zero. This value was estimated based on a sensitivity analysis and parameter calibration (see below). Therefore, for the standard parameter set, forage accessibility decreases

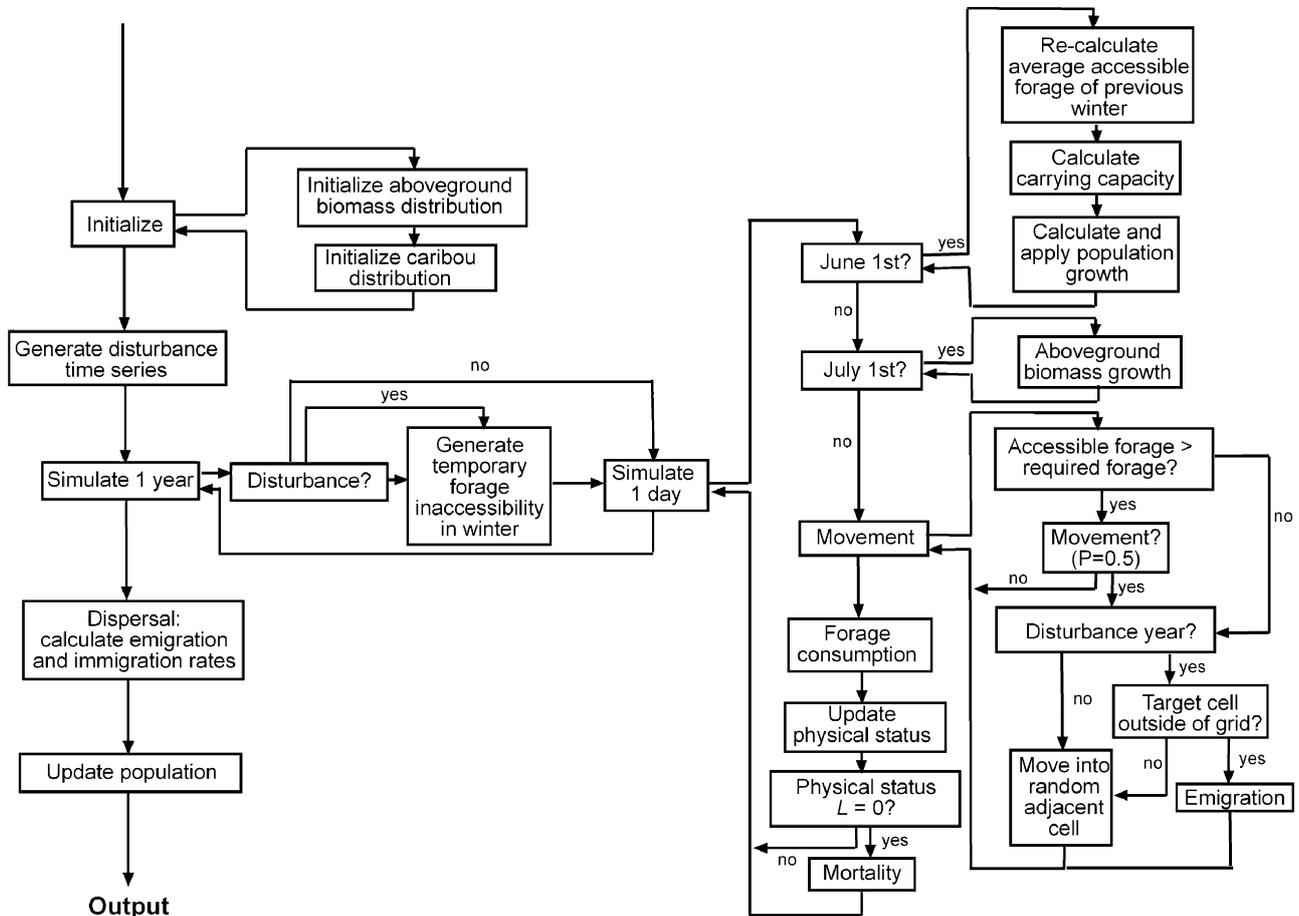


Fig. 1 – Program flow chart of PCSimMod.

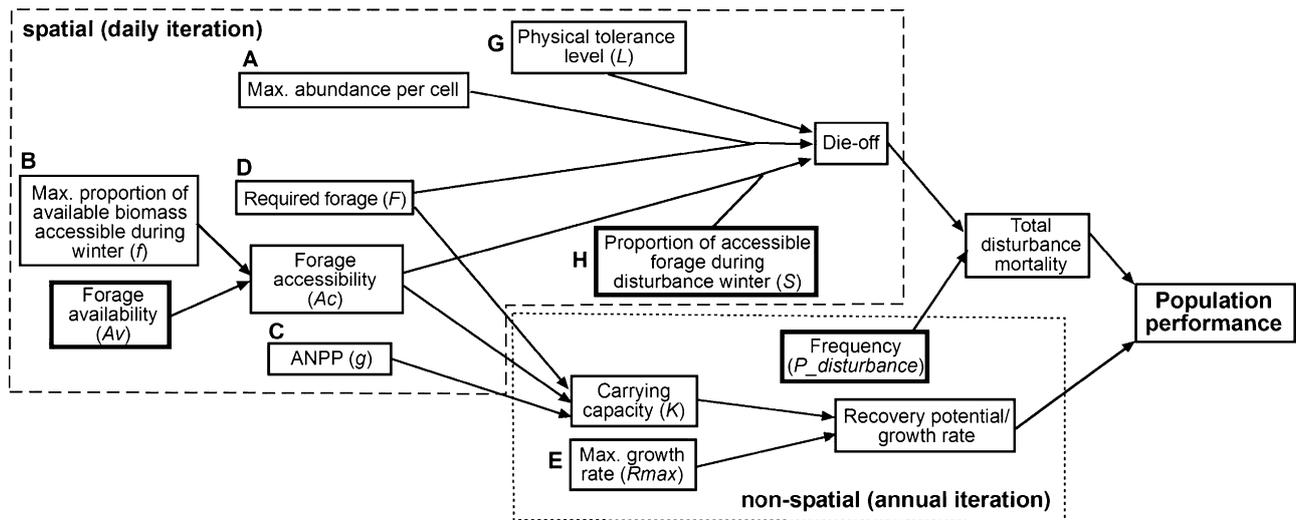


Fig. 2 – Process flow chart of PCSimMod. Bold boxes indicate parameters that were modified for the climate change scenarios. Capital letters indicate the parameters analyzed in the sensitivity analysis (Fig. 4). Information on model parameters are listed in Table 1.

from 26.5% to near 0 for forage availability ranging from 0 to 500 gm⁻².

2.6. Annual net primary productivity (ANPP)

Annual net primary productivity is low in the High Arctic. Productivity–biomass (P/B) ratios range from 3% for polar desert communities to 30% on average for high arctic mires and semi-desert communities (Gould et al., 2003). In the model, the P/B ratio of a cell is linearly related to its available biomass:

$$pb = g \times A_{v(t)(ij)} \tag{6}$$

where *g* is 0.0006 for the standard parameter set (Table 1). Therefore, the pb value ranges from 0 for cells with *A_{v(t)(ij)}* = 0 to 0.3 for cells with *A_{v(t)(ij)}* = 500 gm⁻². Due to inter-annual variation in climatic conditions *g* varies randomly with a CV of 10% (Knapp and Smith, 2001; see Table 1). For example, a low-productive cell (*A_{v(max)(ij)}* = 50 gm⁻², *v* = 0.03) that is reduced to *A_{v(t)(ij)}* = 10 gm⁻² would need approximately 56 years to

completely recover if no further foraging occurs. In contrast, a highly productive site (*A_{v(max)(ij)}* = 500 gm⁻², *v* = 0.3) would need only 8 years to recover following depletion of *A_{v(t)(ij)}* to 100 gm⁻². Each year on the first day of July, vegetation regrowth is applied to each cell up to the maximum amount of biomass availability, *A_{v(max)(ij)}*.

2.7. Forage consumption

Each day caribou consume forage by reducing *A_{v(t)}* in each cell by 2.5 kg caribou⁻¹ from June to September and 1.5 kg caribou⁻¹ during the winter (Parker et al., 2005). The total amount of required forage per individual per year, *F_{total}*, is 660 kg (Table 1).

2.8. Daily movement

On the first day in year 1, the initial number of caribou is distributed in groups randomly across the grid. Each day a group of caribou may stay in a cell or move to an adjacent cell, if forage in the current cell is low or not accessible. The maximum number of caribou per cell, *Abundance_{max(ij)}*, is set at 25 for June to September and 15 for the rest of the year. This is based on observed local densities and annual variation in group sizes; Peary caribou tend to move in smaller groups during the winter (Miller and Gunn, 1978, 1982). As several groups may occur in one cell, the maximum number of individuals per cell is higher than the average observed group size in the field. The probability that a group of caribou in a cell moves out of it is:

$$\begin{aligned} P_{\text{random_walk}} &= 1.0, & \text{if } A_{c(t)(ij)} < \text{Abundance}_{(ij)} \times F \\ P_{\text{random_walk}} &= 0.5 & \text{if } A_{c(t)(ij)} > \text{Abundance}_{(ij)} \times F \end{aligned} \tag{7}$$

where *P_{random_walk}* is the probability of a group moving into one of the eight adjacent cells (randomly chosen). In other

Table 2 – Frequency distribution of aboveground biomass classes for the Bathurst Island complex (BIC) population, based on data from Gould et al. (2003) and GAVM Team (2003)

Biomass class	Range (gm ⁻²)	Relative abundance (%)
1	0–50	65
2	51–100	30
3	101–250	4
4	251–500	1
Average total available forage per cell (gm ⁻²)	49.5	

words, if the amount of accessible forage in the current cell is less than the required forage to sustain the caribou for 1 day, all caribou in that cell will move deterministically; otherwise they will stay with a probability of 50%. For the size of the group leaving the cell we determined the following rule: if the total number of caribou in one cell is less than half of the maximum group size all caribou in the current cell will leave, otherwise only half of them will leave. Over the course of the simulation caribou are not allowed to leave the grid, except during poor winters (i.e., disturbance events), as described below.

2.9. Disturbance

For the standard parameter set we estimated $P_{\text{disturbance}}$, the annual probability of disturbance, to be 0.1, based on four severe winters that caused significant adult mortality in the BIC during the past four decades (Miller and Gunn, 2003) (see Table 1). In disturbance years, i.e., winters with extremely poor forage accessibility, accessibility in each cell is defined by the formula

$$A_{c(t)(ij)} = A_{c(t)(ij)t-1} \times S, \quad (8)$$

where S is 0.0009 for the standard parameter set. To introduce spatial variation in inaccessibility a coefficient of variation of 25% for S is applied for each cell (see Table 1). During disturbance winters caribou will leave the grid if their random walk takes them off the edge of the grid. To allow for disturbance-related die-off events, we assume a maximum number of days that a caribou may survive during winter without consuming sufficient forage based on daily requirements, L ($L=14$, Table 1). Fourteen points are assigned to each individual at the beginning of a simulation. On each day in the winter L is reduced by one point if $A_{c(t)} < \text{Abundance}_{(ij)} \times F_{\text{winter}}$ (i.e., if the individual cannot obtain its daily forage requirement). On a day when $A_{c(t)} > \text{Abundance}_{(ij)} \times F_{\text{winter}}$ the individual will accumulate one point, to the maximum of 14. If $L=0$ an individual will die deterministically due to starvation. Overall, die-off is therefore determined by F (required forage), L (physical status), $\text{Abundance}_{\text{max}}$ (maximum abundance for each cell), A_c (proportion of accessible forage in normal winters), and S (degree of decreased accessibility during disturbance winters) (see Fig. 2). Based on available literature, expert and traditional ecological knowledge, the highest degree of uncertainty exists for the last two parameters; there are no empirical data for either. Using Landsat imagery, Maher (2005) estimated that in April 2003 within three areas where caribou are known to overwinter within the BIC, only 0.49–1.92% of the 30 m × 30 m pixels had less than 50% snow cover. Although this is not directly comparable to the proportion of the land where caribou may be able to access forage, it illustrates the fact that a very high proportion of the forage is inaccessible even during ‘normal’ winters as in 2003. Lacking direct measures of these parameters, we therefore searched for a parameter combination of A_c and S that produced observed average die-off values for the BIC population, as shown in the sensitivity analysis below, and then used this calibration for the standard parameter set.

2.10. Dispersal

Traditional ecological knowledge (Taylor, 2005) and scientific knowledge (Miller et al., 1977; Miller, 1998; Gunn and Dragon, 2002) suggest that caribou occasionally emigrate/immigrate between neighboring populations. Unfortunately, detailed knowledge about the frequency and magnitude of such events is not available. We assumed that emigration events likely increase with increase in the BIC population size and immigration events are random and unrelated to the current BIC population size. To reduce environmental noise we also assumed that, over the course of one simulation run, the net sum of caribou emigrating and immigrating is zero. Therefore, emigration probability, $P_{\text{emigration}}$, increases linearly from 0 to 1.0 until the current population size reaches the carrying capacity K and the probability of immigration equals 18% at all times independent of the population size ($P_{\text{immigration}} = 0.18$). In the standard parameter set both probabilities are annually applied to 5% of the current carrying capacity (dispersal rate $D = 5\%$). For example, in year x with a population of 2000 caribou ($K = 4000$) there is a 50% and 18% probability of emigration and immigration, respectively, that 200 (i.e., 5% of K) caribou emigrate and/or immigrate. This dispersal parameterization introduces a realistic degree of stochasticity to the population by ensuring a balanced number of emigrating and immigrating caribou over the course of one simulation run.

2.11. Sensitivity analysis

Observed changes in BIC population size from 1985 to 2001 were used to parameterize the standard parameter set (Fig. 3). We neglected the survey data before 1985, due to the presence of >10 year gaps between two survey years. To parameterize the model we conducted a sensitivity analysis for eight parameters (Fig. 4). Each parameter was systematically varied while all other parameters were kept constant. Simulations were repeated 100 times for each parameter combination for 1985–2001 with 727 initial caribou as observed in 1985. To measure die-off sensitivity we calculated the deviation from the 70% population die-off observed for three consecutive disturbance winters during 1995–1997 (Miller and Gunn, 2003). To measure sensitivity regarding post-disturbance recovery we calculated the average deviation from observed population abundance for the years 1993 and 1994 where the BIC population reached a peak before the population crash (1993 = 2387, 1994 = 3011; see also Fig. 3).

2.12. Climate change scenarios

The standard parameter set of PCSimMod was developed to provide a realistic simulation model with the best available knowledge, to use as a baseline comparison with potential scenarios of climate change. We were interested in detecting parameter combinations where either positive or negative effects of climate change begin to prevail. Climate change-related effects that we considered include (a) an increase in the frequency of disturbance events ($P_{\text{disturbance}}$), (b) an increase in the proportion of inaccessible forage during disturbance (S), and (c) an increase in available aboveground biomass due to a longer and warmer growing season ($A_{v(\text{max})}$). We assumed

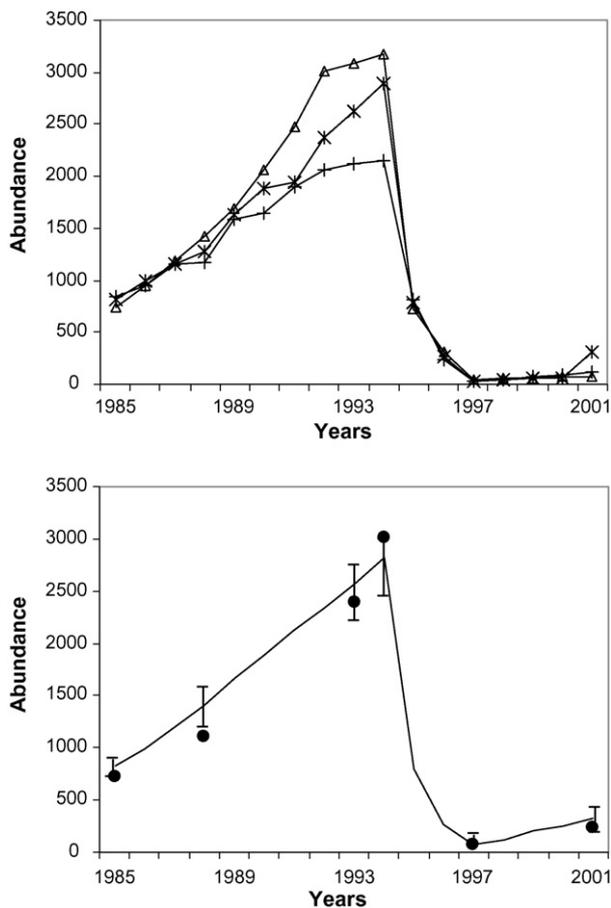


Fig. 3 – Upper panel: Three typical simulation runs. Lower panel: Available survey data for the Bathurst Island complex (BIC) population (dots) and average population size for 100 simulation runs of the standard parameter set with standard deviations for 1985–2001. Population survey data are from Miller (1987, 1989, 1995, 1998), Gunn and Dragon (2002) and Ferguson (unpublished data).

that these parameters will gradually increase over the course of 100 years.

2.13. Increase in available biomass under climate change ($A_{v(max)}$)

Using a nutrient-based plant community model, Epstein et al. (2000) estimated that current climate change trends for the High Arctic may lead to a 50% increase in aboveground biomass over 100 years. We therefore implemented three scenarios with a gradual increase of 25%, 50% and 75% in $A_{v(max)}$, respectively. Note that for annual net primary production v cannot exceed 0.3 (see 'Annual net primary productivity'), but allowed $A_{v(max)(ij)}$ to increase above 500 g m^{-2} over the course of a climate change trajectory.

2.14. Increase in disturbance-related forage inaccessibility (S)

Potential changes in the severity of disturbance winters were modeled by gradually decreasing S over the 100 years of simu-

lated time. Together with the general forage accessibility in each cell (A_c), the required forage (F), the maximum abundance per cell, and the physical tolerance level (L), S strongly determines the severity of population die-off after each disturbance event (Fig. 2). In the standard parameter set S equals 0.0009, i.e., 99.91% of the forage that is accessible in normal winters becomes inaccessible during disturbance winters (see sensitivity analysis). For the climate change scenarios we gradually decreased the S value over the course of 100 years (i.e., decreased forage accessibility during disturbance winters). The maximum applied decrease of S was 75% of the initial value (i.e., forage accessibility decreased from 99.91 to 99.97%).

2.15. Increase in the probability of disturbance events ($P_{disturbance}$)

As a third climate change parameter we gradually increased the probability of disturbance over the 100 year simulation. For the climate change scenarios we applied average return intervals of 10 years ($P_{disturbance} = 0.1$), 8 years ($P_{disturbance} = 0.125$) and 6.6 years ($P_{disturbance} = 0.15$). In other words, for the second of the latter three scenarios the probability of disturbance would be 10% in year 1 and increases to 12.5% in year 100; in the third scenario, it increases to 15% in year 100. As model output we calculated the relative change in EMA based on the standard parameter set ($EMA_{new}/EMA_{standard}$; where $EMA_{standard} = 123$).

3. Results

3.1. Movement patterns

Movement patterns generated by the model could not be validated as longer-term, detailed (i.e., daily) movement behavior of Peary caribou is currently not available. However, the simulated distances of annual movements correspond well with estimated movement ranges of Peary caribou on the BIC (Miller, 2002; Ferguson, personal communication): 90% of all simulated caribou groups had an annual movement range of 70–210 km. On average groups encountered 1.2 edge cells over the course of one simulated year.

3.2. Sensitivity analysis and standard parameter set

We used the survey data of the BIC population from 1985 to 2001 to calibrate the standard parameter set (Fig. 3 and Table 1). To analyze the model behavior we then varied a set of eight parameters in a sensitivity analysis (Fig. 4). Each parameter was systematically varied while all other parameters were kept constant. We found that population die-off (dotted lines in Fig. 4) was most sensitive to maximum abundance in each cell ($Abundance_{max}$), forage accessibility (f), required forage (F), and forage accessibility during disturbance (S). Die-off was much less sensitive to maximum growth rate (R_{max}) and the physical status (L_{init}). Variation in the dispersal rate (D) had no effect on either die-off or population increase (Fig. 4).

For the sensitivity analysis of population sizes during recovery (solid lines in Fig. 4) an increase in forage accessi-

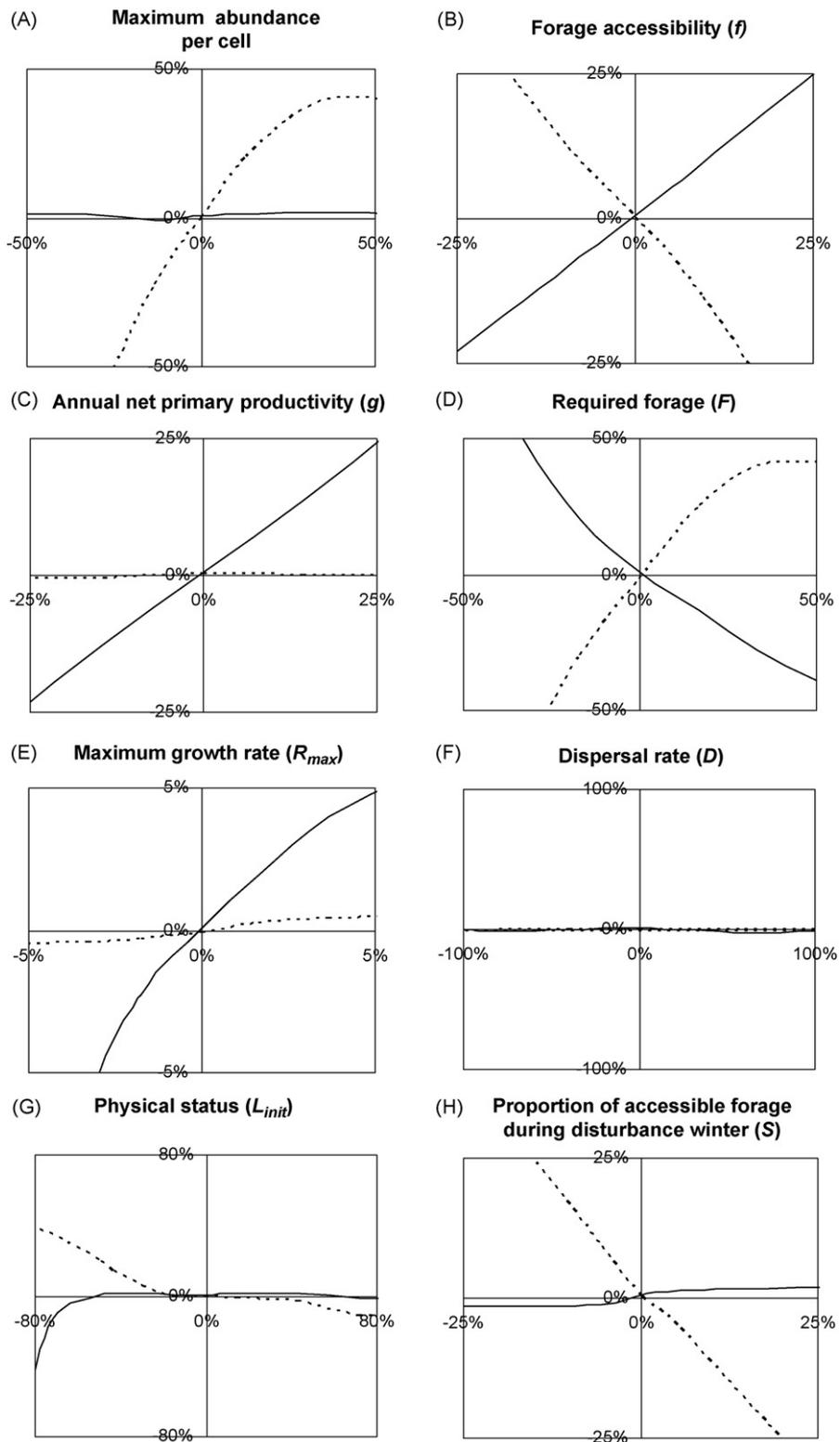


Fig. 4 – Results of the sensitivity analysis for eight model parameters. Each parameter was systematically varied while all other parameters were kept constant at their standard values. Dotted lines represent the variation in average die-off relative to average die-off of three consecutive disturbance winters, 1995–1997 (average die-off 70.5%). For example, an increase of 10% and 41% on the y-axis indicates an average die-off of 78% and 100%, respectively). The solid line shows the resulting average deviation from population abundance for the years 1993 and 1994 (Fig. 3). For panel A and D note that the increase in die-off levels off at 100%.

bility (f) and annual net primary productivity (g) resulted in a linear increase of simulated population sizes and a non-linear positive response in maximum growth rate (R_{max}). When the amount of required daily forage (F) increased average simulated population sizes decreased. Overall, sensitivity was less for maximum abundance per cell, physical status L and the proportion of accessible forage during disturbance winters (S). However, when the initial L value was reduced to less than 5 points (i.e., >65% relative decrease from the maximum of 14), the population size responded strongly negatively. In this case even during normal winters individual caribou would risk starvation if they subsequently encountered several grid cells with low forage availability or accessibility.

A typical simulation run for the standard parameter set (Fig. 5) shows that accessible aboveground biomass decreases during phases of significant population increase and then may recover afterwards. Die-off values for disturbance years averaged 70%, similar to average die-offs for 1995–1997. The carrying capacity K also varies between years. However, because of a feedback mechanism between the annual population growth rate and K it remains within a particular range. This is due to the fact that the growth rate is a function of K and that K is annually re-calculated depending on the amount of available and accessible forage (which in turn is influenced by population size, i.e., the annual growth rate).

3.3. Results of climate change scenarios

Increase in biomass strongly decreased population die-off because caribou were less prone to starvation (Fig. 6, lower line). For example, a 25% increase in biomass resulted in a population die-off of 22%. In contrast, a similar increase in forage inaccessibility during disturbance years increased die-off to almost 100% (Fig. 6, upper line).

As expected, a lower population die-off resulted in an increase in the expected minimum abundance. Relative changes in expected minimum abundance increased with increasing biomass and were only slightly affected by an increase in the probability of disturbance events (Fig. 7). Thus, if the proportion of inaccessible forage during disturbance winters remained at 99.91% (i.e., $S=0.0009$), an increase to more than 8% of the initial biomass resulted in a positive effect of climate change, even if disturbance frequencies were relatively high (i.e., 0.15). For example, a 25% increase in biomass over the course of 100 years generated an expected minimum abundance approximately two times higher than in the standard scenario (i.e., 250 caribou), despite an increase in the average frequency of poor winters from 10 to 12.5 years.

For the overall set of parameter combinations the net effects of climate change for the BIC population varied from strongly positive to strongly negative effects, relative to the predictions of the standard parameter set (Fig. 8). Comparing the relative importance of all three climate change parameters, we found that the frequency of disturbance events had the lowest impact, followed by changes in biomass and forage accessibility during disturbance events. For a 25% increase in biomass over 100 years net effects of climate change were negative if inaccessibility during disturbance winters increased by more than 25%. For a projected 50% increase in biomass this changed to 40% for the current disturbance probability

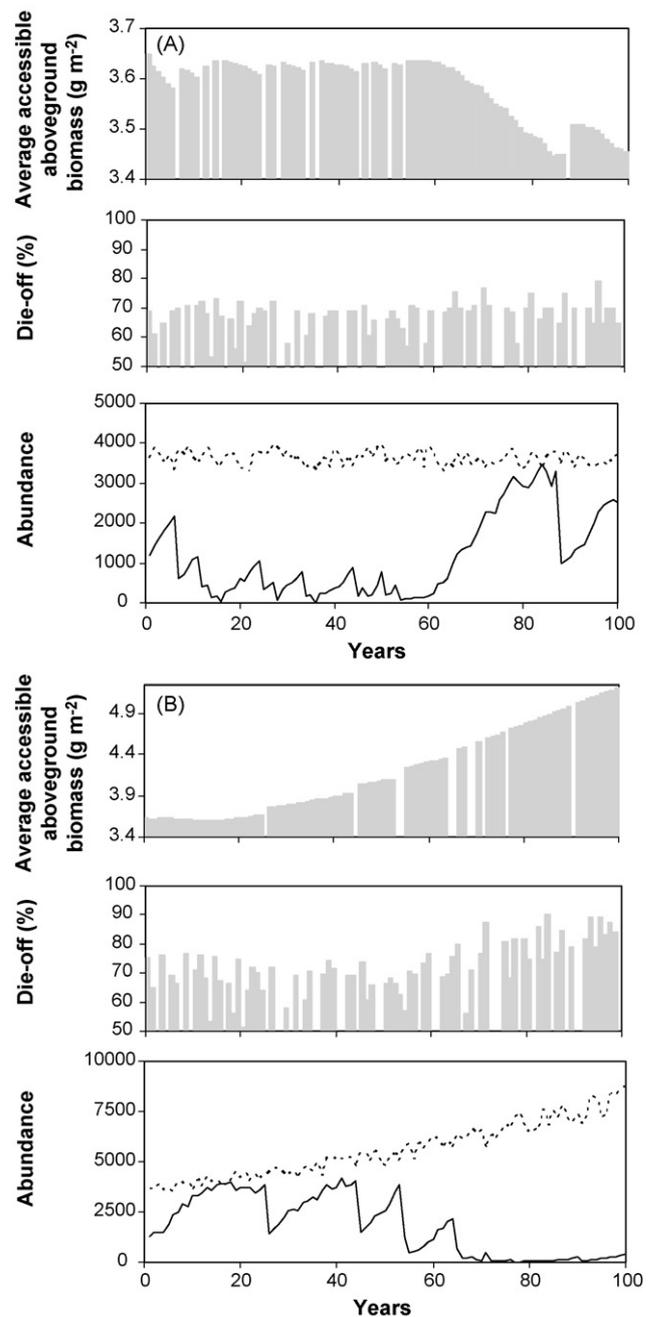


Fig. 5 – Typical simulation run for the standard parameter set (A) and a climate change scenario (B). For the climate change scenario aboveground biomass increased by 50% over 100 years, average disturbance return interval was reduced from 10 to 8 years (i.e., $P_{disturbance} = 0.1$ to 0.125) and proportion of accessible forage in disturbance winters (S) from 0.0009 to 0.000575. Upper panels for A and B show the average amount of accessible forage during mid-winter; disturbance years are indicated by blank areas showing temporarily inaccessible forage (one simulation run). Each mid panel shows the average annual die-off for 10 simulation runs. The lower panels show the carrying capacity (dashed upper line) and population abundance (solid lower line) (one simulation run). Population die-offs occur in disturbance years with temporarily inaccessible forage.

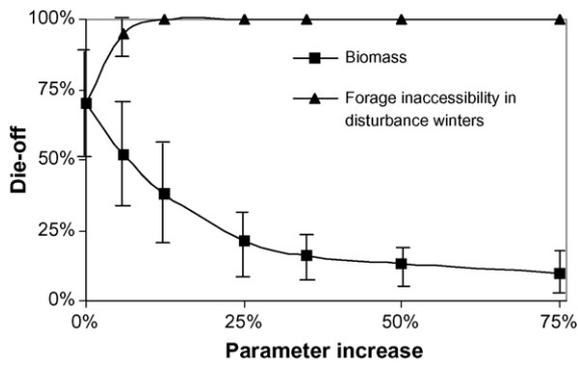


Fig. 6 – Average population die-off following disturbance winters (standard deviations for 100 replicate simulation runs). The upper line shows the resulting die-off when inaccessibility during disturbance winters was increased from 99.91 to 99.98% (i.e., relative decrease in parameter S from 0.0009 to 0.000225). The lower line shows the response for a relative increase in biomass up to 75% (i.e., increase in $A_{v(max)}$). Both parameters were varied independently.

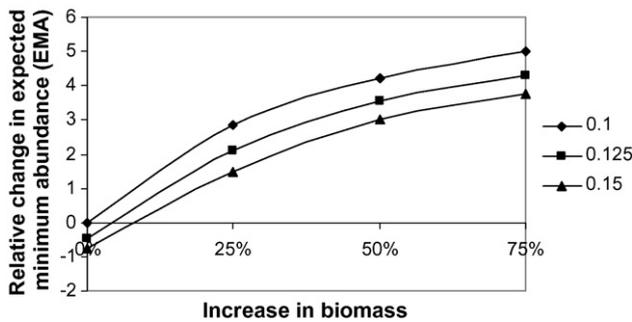


Fig. 7 – Relative change in expected minimum abundance (EMA) for increases in biomass and annual disturbance probability (100 simulation runs). For example, for the 50%/0.15 scenario, biomass in each cell (i.e., $A_{v(max)(ij)}$) increased to 50% of the initial value over the course of 100 years. Simultaneously, annual probability of disturbance (i.e., $P_{disturbance}$) increased from 10% at $t=1$ to 15% at $t=100$. Proportion of forage accessible in disturbance winters was the same as in the standard parameter set ($S=0.0009$).

and 31% if disturbance probability increases to 15%. If biomass increases to 75% within the next 100 years Peary caribou would benefit from climate change, unless inaccessibility in disturbance years increases by more than 46%.

4. Discussion

Our model suggests that Peary caribou in the BIC will experience significantly lower population die-offs if biomass increases by 50% as projected (Epstein et al., 2000), and if the currently estimated proportion of inaccessible forage during disturbance winters does not change with climate change. However, if forage inaccessibility during disturbance winters increases over the next 100 years, caribou may experience

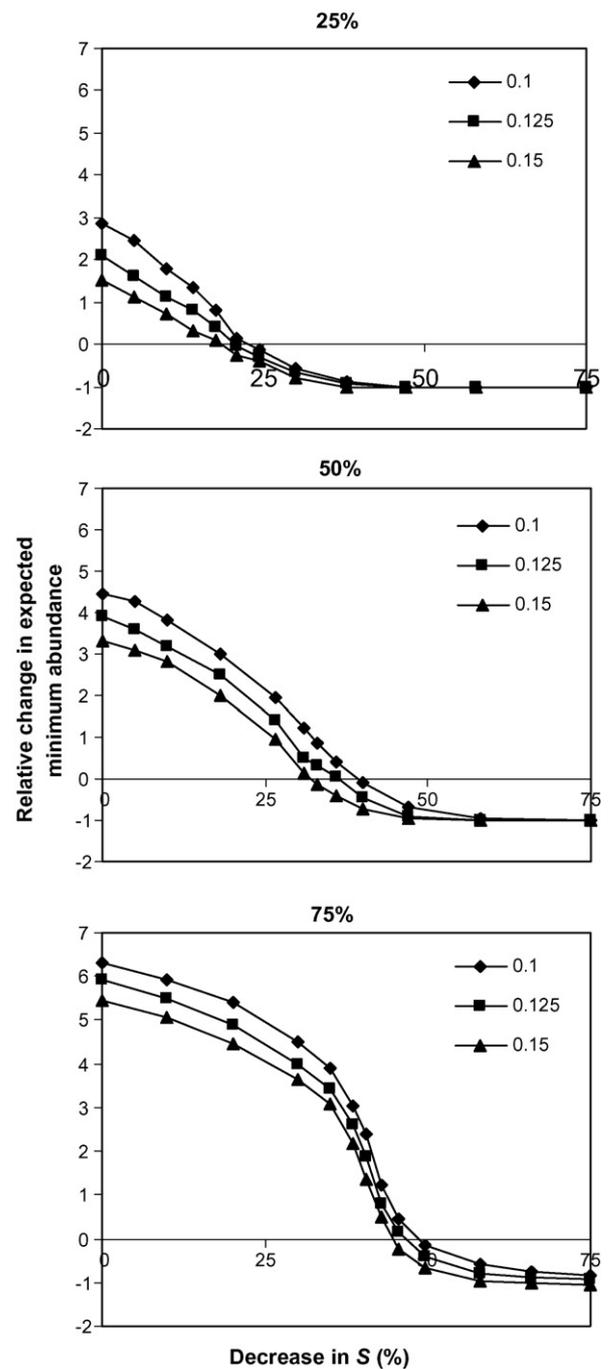


Fig. 8 – Relative change in expected minimum abundance (EMA) for an increase in annual disturbance probability and decrease in proportion of forage accessible in disturbance winters, for three different scenarios of biomass increase (25%, 50%, 75%) (100 simulation runs). For each scenario, parameters were incrementally increased from $t=1$ to $t=100$. Note that negative changes in EMA reach a maximum at -1 (i.e., 100% reduction) when population abundance is near 0.

negative net effects of climate change, even if aboveground biomass increases proportionally more than forage inaccessibility. Decrease in forage accessibility during disturbance winters tends to have a stronger impact on population dynamics than increase in biomass availability as forage accessibility indirectly governs mortality (Fig. 2). If an increase in the frequency of extreme climate events occurs as projected (ACIA, 2005), our model suggests that this may have a lower impact on Peary caribou population dynamics than potential increases in the severity of disturbance events. This is due to the fact that caribou are able to recover relatively quickly after a population crash (see Tews et al., 2007). Thus, future increases in population die-offs could indicate a large threat even if biomass becomes more available. Unfortunately, there is currently a lack of knowledge with regards to how much forage is accessible in 'normal' and 'poor' winters. Even more unknown is whether and how this may change under climate change.

In this paper we have not dealt with the issue of forage quality and the fact that Peary caribou are selective grazers and do not use all accessible biomass. The forage of Peary caribou includes gramminoids, forbs and dwarf shrubs (Shank et al., 1978; Thomas and Edmonds, 1983) with a preference for patches with shallow or no snow where fruticose lichens and *Luzula* spp. occur (Thomas et al., 1999). The calibrated standard parameter set required a very high degree of forage inaccessibility to generate observed population dynamics. Inaccessibility during disturbance winters was over 99.9% on average. We do not actually know how much of the range is inaccessible in extremely poor winters and are therefore not able to validate this estimate with empirical data. Forage accessibility depends on multiple weather factors, making predictions difficult without direct monitoring of snow cover within caribou wintering areas. We suggest that the high proportion of inaccessibility may only apply to the actual forage plants that Peary caribou use and, thus, overall biomass accessibility during disturbance winters may be significantly higher.

Even though our model represents our best educated guess, there are, of course, several uncertainties. For example, we have not dealt with ecological interactions based on food web dynamics (see e.g., Megrey et al., 2007). Climate change may affect other High Arctic species such as muskox, arctic wolf and arctic mainland caribou which may change the interactions among these species and between these species and Peary caribou, resulting in indirect effects of climate change on Peary caribou. Moreover, Peary caribou may suffer from increased insect harassment if summer precipitation and temperature increase (Toupin et al., 1996).

4.1. Conclusions and outlook

Since 1975, Inuit in the Canadian High Arctic have faced challenges of local declines in populations of Peary caribou, a species critical to culture and nutrition; they have done so through self-imposed harvesting restrictions to conserve caribou populations. This study has provided a first modeling assessment for the effects of climate change on this ecologically and socially important species. Further studies are needed to assess the potential impact of climate change on ecological systems, and to adequately conserve and manage this and other species.

Currently, there are only a few other studies that simulate the effects of climate change on wildlife species (e.g., Reuter and Breckling, 1999; Coulson et al., 2001; Wichmann et al., 2003; Tews and Jeltsch, 2004; Tews et al., 2006). Individual-based models (IBM) (e.g., Grimm et al., 2005) have emerged as a useful tool since they are capable of detecting climate-related effects that may translate from the individual to the population level. For example, in an IBM study on the European robin (*Erithacus rubecula*) Reuter and Breckling (1999) found that reproductive activities in relation to temperature and caterpillar emergence are detectable on the individual level more precisely than on the population level.

In climate change research one of the greatest challenges is to deal with public expectations for fairly precise predictions about how particular populations and ecosystems will respond to future climatic changes at regional levels. In most cases one is faced with sparse empirical data and a wide array of questions. How can we bridge this gap? We believe one valuable approach is to build species simulation models that are based on simple ecological rules and which are capable of assessing whether and how population dynamics are likely to depart from current conditions. This allows for transparency and for communicating ecological models beyond the scientific community.

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