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MODELING

A Model for Assessment of Northern Caribou Population Response to Projections of Seasonal Range Conditions and Predation Risk

Model Description & Outputs for Sensitivity Analysis and Testing

Draft

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This report builds on an earlier draft, and therefore much of the introduction and methods section are taken from the following report:

Sutherland, G.S., D. O'Brien, and R.S. McNay. 2004. Caribou Habitat Assessment and Supply Estimator (CHASE): Prototype Seasonal Range - Population Models for the Northern Caribou.



Introduction

Current prediction of the ecological value of northern caribou ranges is based on the Caribou Habitat Assessment and Supply Estimator (CHASE) framework (McNay and Zimmerman 2002). Several range types are considered in this framework: 1) calving and summer range; 2) pine-lichen winter range; 3) high-elevation winter range; and 4) movement corridors. Each range type is influenced by the risk of predation by wolves, for which wolf density was estimated based on its relationship to moose density.

The objective was to develop a conceptual model for projecting populations of Northern Caribou in the Mackenzie area of B.C. using the projected habitat quality and predation risk indicators from the CHASE seasonal range models, and population parameters measured from the area. This involved simulating a population by randomly sampling demographic and environmental variables from defined probabilities and then analyzing their cumulative effects on the state of the population over time. Model needs to capture the response of the population to changes in the distribution and amount of habitat within each seasonal range type. Therefore a spatial population model was necessary.

This report provides documentation on significant modifications made to the conceptual model for spatial population modeling for the northern caribou population model, as well as a description of the semi-spatial stage based population model prototype developed for efficient model testing and sensitivity analysis. Included in the report are the results from a series of sensitivity analyses designed to test model response to various parameter states. Specifically, I tested the response of the model to 1) static vs. dynamic landscape; 2) density dependant mortality in avoided habitat; 3) sensitivity to systematic variation in annual vital rates; 4) sensitivity of the model to systematic variation in carrying capacity in each habitat category; 5) response to different partitioning of annual mortality among seasonal ranges; 6) response to varying the proportioning of mortality in predation risk classes.



Methods

Study Areas

The general study area for the Omineca Northern Caribou Project is located in the Mackenzie TSA in northern BC. This TSA covers 61 million hectares, includes all of the Mackenzie Forest District, and is located within the Omineca subregion. Within the TSA, areas used by caribou herds (i.e., the Wolverine, Chase/Sustut, and Akie/Ospika herds) have been delimited and form the basis for inventory and monitoring studies since 1998 (Figure 1). These herd areas cover approximately 25,503 km² and are generally equivalent to those areas depicted by the Ministry of Sustainable Resources Management. This study focuses on the Wolverine Study Herd.

Landscape units associated with the 3 study areas are as follows:

Wolverine: Manson, Klawli, Germansen, Wolverine, Upper Omineca, Lower Omineca, Discovery;

Chase/Sustut: Upper Osilinka, Lower Osilinka, Tenakihi, Mesilinka, Factor Ross, Carina Tomias, Swannell, Aiken, Upper Ingenika, Lower Ingenika, Thutade; and

Akie/Ospika: Collins, lower Ospika, Upper Ospika, Davis, Chowika, Pesika, Lower Akie, Upper Akie, Paul, Kwadacha.

Ecoregions included in the three study areas are the Skeena and Omineca Mountains Ecoregions, and Biogeoclimatic zones include SBS, ESSF, AT and BWBS.

Generally, all three herd areas are characterized by mountainous terrain with extensive alpine habitat, large river valleys, and dense coniferous forests. Much of the Engelmann Spruce-Subalpine Fir (ESSF) and Spruce-Willow-Birch (SWB) biogeoclimatic zones of these study areas are characterized as ecosystems with infrequent stand-initiating events, such as wildfires, with a mean disturbance return interval of 200 years (B.C. Ministries 1995). By comparison, the Boreal White and Black Spruce (BWBS) and Sub-boreal Spruce zones (SBS) are characterized as ecosystems with frequent stand-initiating events, with wildfires reaching sizes of tens of thousands of hectares and a mean return interval of approximately 125 years. The resulting landscape is a mosaic of even-aged stands of different ages (B.C. Ministries 1995).

Northern caribou are relatively abundant in BC (approximately 16,000 animals), and tend to occur in the mountainous western and northern parts of the province, wintering in mature low elevation lodgepole pine or black spruce forests or high wind-swept slopes (Heard and Vagt 1996). Heard and Vagt (1996) recognised 28 distinct herds of northern caribou, 10 of which at least partially reside in the Mackenzie TSA. Currently, MSRM and MWLAP recognizes a total of 7 herds of northern caribou, and 1 herd composed of both northern and mountain caribou reside in the Mackenzie TSA. Population data for these herds are listed in Table 1.

**Table 1. Estimated population sizes and population status for caribou herds in north-central British Columbia. Source: Zimmerman et al. (1999)**

Herd	Population Size	Population Status	Reference
Frog/Gataga	400-1200	unknown	Heard & Vagt 1996
Upper Finlay	500-1000	unknown	
Akie/Ospika	200-500	unknown	
Chase/Sustut	600-800	stable / slowly declining	Wood 1996
Graham	800	unknown	Heard & Vagt 1996
Wolverine	300-400	stable / slowly declining	Wood 1998
Scott/Blackwater	50-200	unknown	
Misinchinka	100-250	unknown	

Northern caribou feed primarily on terrestrial lichens. The species preferred by caribou as forage are dominant in lichen-bearing forest types ranging from approximately 40 to 140 years. As these stands age and the canopy closes, these lichen species are then replaced by moss, reducing the usability of the stand to caribou. Several forest types in the Mackenzie Timber Supply Area (TSA) have sufficient densities of lichens to provide suitable habitats for Northern caribou including: lodgepole pine (*Pinus contorta*) or black spruce (*Picea mariana*) forests at low elevations; high-elevation Engelmann spruce (*Picea engelmanni*) and Sub-alpine fir (*Abies lasiocarpa*) forests in the EFFF/AT BEC zones (see Section 2.3 for detailed description). Much of the Mackenzie Timber Supply Area (TSA) is comprised of high to medium value caribou habitat (64 %).

Northern caribou herds are subject to predation by wolves, and grizzly bears. Bergerud and Elliot (1986) suggest that colonization of interior B.C. by moose (*Alces alces*) during the 1900's has resulted in increased wolf (*Canis lupis*) populations and lead to higher predation rates and population declines in caribou (*Rangifer tarandus-caribou*). Caribou often use high elevation habitats in winter where they are spatially separated from moose and wolves that tend to remain in valley bottoms (Seip 1992). During the summer there can be some range overlap between caribou, moose and wolves, but caribou are predominantly spatially segregated from wolves as they tend to occur in rugged mountain terrain (Seip 1992). This segregation typically results in low adult mortality rates and relatively high calf survival rates into the fall, possibly as a result of reduced wolf predation.

Concerns exist that Northern caribou populations in the Omineca region could become exposed to similar ecological conditions that have apparently caused declines in Mountain caribou populations elsewhere in B.C. These concerns are of three types:

1. Movement patterns between the different range types (in particular spring and fall movements through low elevation ranges) have the potential to position caribou in direct or proximal contact with those ranges occupied by moose and wolves. In addition, increasing road and cutblock networks may increase hunting, poaching and predator access into higher quality habitats. Recent studies in northeastern Alberta have shown that wolf movements and predation on boreal woodland caribou are facilitated by linear corridors such as roads, pipelines and seismic lines (James and Stuart-Smith 2000, Dyer et al. 2001).



2. Silvicultural regimes based on clear-cut logging can cause a variety of impacts to caribou, such as reducing the distribution of stands of sufficient age that permit sufficient accumulation of biomass of preferred lichen species. Stand conditions permitting sufficient accumulation of terrestrial lichen biomass are dependent on overstory and understory development, canopy structure, and patch sizes, which are in turn dependent on the natural disturbance regime in these forests. Furthermore, increases in the density and spacing of early successional clearcuts can result in increased moose forage in areas surrounding caribou habitat. Several studies suggest wolves "follow" moose into these early successional clearcuts, and where their distribution overlaps, caribou are subjected to increased predation rates (Bergerud 1985; Seip 1985; Darby and Duquett 1986; Seip 1992; Smith *et al.* 2000; James 1999)
3. There are indirect effects of disturbances to individual caribou due to increased industrial activity in the area (Dyer 1999; Dyer *et al.* 2001). James and Stuart-Smith (2000) indicate that when compared to random locations, wolves occupy areas closer to linear corridors, and caribou killed by wolves occur closer to linear corridors, while surviving caribou occupy areas away from linear corridors, where the average amount of displacement from random is about 100m. Furthermore, caribou experience increased movement in response to industrial development, which results in increased energy expenditure (Murphy and Curatolo 1987; Bradshaw *et al.* 1997; Dyer 1999), and the cumulative stress negatively effects calf production and survival (Miller *et al.* 1972; Bradshaw *et al.* 1998). Some authors have suggested that caribou may become habituated to roads and other disturbances in migratory corridors or non-calving areas of their home range, which may lead to increased mortality from vehicle collisions (Klein 1971; Miller *et al.* 1972). There is also evidence that caribou become displaced with the presence of roads in calving grounds (Dau and Cameron 1986).

Population Structure and Demography

Historical census information on the Wolverine herd is sparse. The most recent demographic data used in this report is based on 3 years of telemetry monitoring (1999-2001) for a total of 70 radio-collar-years of data (see refs). Four age classes were distinguished in these studies: calves (< 1 year), yearlings (1 to < 2 years), juveniles (2 to < 3) years, and adults (> 3 years). A total of 54 calves, 4 yearlings, 3 juveniles, and 63 cows were radio-collared, and their movements and mortalities were determined, along with recruitments to the herd.

The current age class structure of the population results from conditions that occurred during the time period leading up the current data set. Rather than specifying the proportion of animals in each life stage from the current data, the proportions of animals at each life stage were determined by calculating the stable age class distribution based on vital rates obtained from the 1999-2002 data (Table 2).

**Table 2. Estimated proportion of the population in each life stage.**

Life Stage	Proportion of Population
Calves	0.188
Yearlings	0.099
Juveniles	0.092
Adults	0.616

Observed Demographic Data for the Wolverine Herd (1999-2001)

Current estimates are a total herd size of 450 animals. Data shows that 85% of adult cows give birth to calves (i.e. no births were observed among yearlings and juveniles), with an observed fecundity rate of 0.388 calves/female (data pooled over all years) assuming a 1:1 sex ratio in the population. During the monitoring period, 12 deaths were recorded for adults, and 26 deaths among calves. These lead to the following annual survivorship estimates: survivorship of adults $S_a = 0.99$ (observed range: 0.98 – 1.00); survivorship of juveniles and yearlings pooled $S_j = 1.0$ (no annual variation); survivorship of calves $S_c = 0.48$ (observed range: 0.36 – 0.55; Table 3). These rates imply a mean annual rate of population increase λ of 1.094 (calculated range: 1.065-1.112) suggesting a stable or increasing population size.

Table 3. Estimated annual survivorship by life stage for the Wolverine Herd (1999-2001). Estimates of variation for survivorship are based on data reported in Gaillard et al (1998).

Vital Rate	Calves	Yearlings	Juveniles	Adults
Survivorship	0.48	1	1	0.99
CV	0.15	0.15	0.15	0.05

Estimated Age-Specific Demographic Rates for the Wolverine Herd

Because of the limited samples of data (in particular short time period), the above rates have been supplemented by expert opinion (McNay *pers. comm.*) and estimates from the literature to generate the age-specific vital rates and other demographic parameters used in the models. Estimates of variability were obtained from Gaillard et al (1998). The results are presented in Table 3.

Sex Ratio

There is no indication that a 1:1 sex ratio for the population cannot be assumed. This assumption is strongest for calves and juveniles in the data from the Wolverine Herd.

Age-specific Fecundity

Current data (1999-2001) indicates that 84% of adult females have calves. Because this is likely an underestimate (there is some early mortality not detected in the telemetry data), the current best estimate is 90%. About 25% of juveniles have calves, while yearlings do not. Estimated stage specific fecundity rates are given in Table 4). Longevity is estimated at 15 years, and estimates of the generation time $G_t = 9$ years based on these results.

Table 4. Estimated annual age-specific fecundity for components of the Wolverine Herd. Variance estimates for Adult females taken from 1999-2001, and corrected for sampling bias according to the methods in Burnham et al. (1987). Variance for Juveniles estimated at 10%. Source: McNay (*pers. comm.*)

Vital Rate	Calves	Yearlings	Juveniles	Adults
Fecundity (Adult Females)	0	0	0.25	0.9
CV	0	0	0.025	0.1161

Seasonal Ranges

In the Mackenzie TSA, Northern Caribou move seasonally (Figure 1) among a number of stand types dispersed geographically through each of the study areas. At present, four Northern caribou range types are considered by the CHASE framework: Calving & Summer Range (CSR), Pine-Lichen Winter Range (PLWR), High Elevation Winter Range (HEWR), and Movement Corridors (CORR).

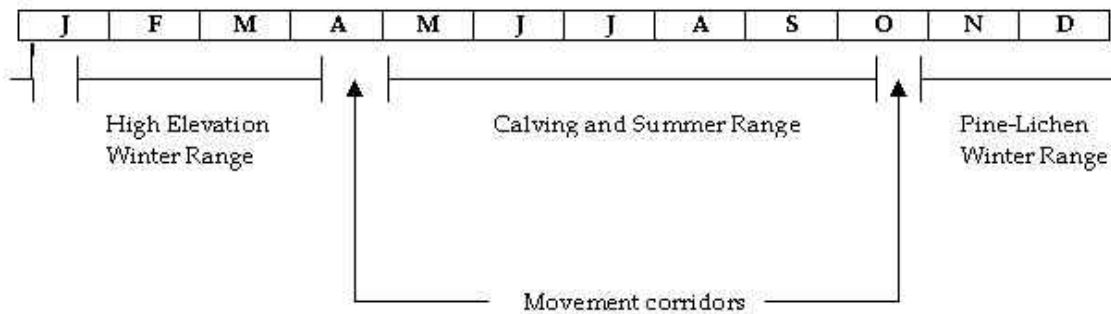


Figure 1. Seasonal ranges and periods of their use by the Wolverine herd. Note that dates shown below are approximate, and the herd displays considerable year-to-year variation in range use and timing of movements. Adapted from Remesz (2002).

Range Descriptions

The summary descriptions below are taken from CHASE (2003). For ecological background, and details on how each range type is modeled in CHASE, refer to that document.

Calving & Summer Range: Northern caribou typically can be found at high elevations in the upper Engelmann Spruce - Subalpine Fir (ESSF) or Alpine Tundra (AT) biogeoclimatic zones during the “calving” period (May-June), when cows usually make prenatal movements to seek individual sites for calving, and “summer” period ending in the fall (September-October) when they aggregate into large groups following mating (CHASE 2003). On these ranges, herds tend to be dispersed geographically, and this behaviour is widely considered to be an anti-predator tactic.

The Calving and Summer Range (C_SR) submodel therefore characterizes habitat used by northern caribou in terms of relative preference they demonstrate for specific conditions during the natal period and throughout summer. The ecological factors considered to have the greatest influence on habitat value were percent slope, ecological unit, and forest inventory group.

Pine-Lichen Winter Range: Relatively open, dry, nutrient-poor pine-lichen woodlands provide an important foraging opportunity for Northern caribou in early winter before significant snows accumulate (Nov.-Jan), such that caribou can crater through the snow to access terrestrial lichens. Lichen species utilized in these stands are collectively known as reindeer lichens.

In the Pine-Lichen Winter Range (PLWR) submodel, the preference that caribou likely exhibit for an area is primarily influenced by the value of the habitat to caribou. The ecological factors considered to have the greatest influence on habitat value are elevation, terrestrial lichen habitat capability, stand characteristics, and forest floor characteristics.

High Elevation Winter Range: Northern caribou leave pine-lichen winter ranges in search of high-elevation winter ranges presumably in response to the increasing difficulty they experience in negotiating snow at low elevations as snow packs increase in depth and density through the winter. If herds move to high-elevation winter ranges, they usually do so after January in late winter, before they make distinct movements to low-elevation habitat during spring. Herds tend to be relatively concentrated geographically in these ranges, seeking specific and localized areas free from snow due to scouring by persistent and strong winds. Such wind-blown areas persist primarily along ridges within the Alpine Tundra (AT) biogeoclimatic zone and selection of this habitat may be displayed strongly by some herds or strongly only in some years

The High-elevation Winter Range (HEWR) submodel characterizes habitat used by Northern caribou in terms of the relative preferences they demonstrate for specific conditions that sometimes occur during the middle and late-winter period. Avoidance of predators and forage availability were considered the most proximate life requisites for northern caribou during the late-winter period. High elevation areas capable of allowing caribou access to either terrestrial lichens or arboreal lichens were considered to encompass the ecological factors of critical importance to the HEWR submodel. Use of this range type is not strongly defined seasonally because northern caribou's reliance on this range has extreme annual variation.

Movement Corridors: During their annual cycle, caribou often move from one seasonal range to another along distinct corridors. Availability to accessible forage, avoidance of moose and thereby wolves are considered the primary reasons caribou move. Caribou also demonstrate a lack of fidelity to their winter ranges, presumably to allow range rotation to reduce grazing pressure on slow-growing terrestrial lichens (Bloomfield 1980). It is possible that caribou continue to explore new areas, using new movement corridors throughout their lives.

Movements between PLWR and HEWR are typically along valley bottoms, and mountaintops are avoided. These corridors are predominantly forested habitats with high timber values and relatively easy terrain to access. With the potential for interactions between forest harvesting practices and caribou habitat requirements, it is



therefore important to be able to model corridor locations to ensure these areas are managed appropriately.

The Movement Corridor (CORR) submodel characterizes the factors affecting the corridors that northern caribou use to move between pine-lichen winter ranges and high-elevation winter ranges. Topographic position and predation risk were the ecological factors considered most important in influencing the selection of movement corridors. Unlike the other range types discussed above, habitat type (e.g. ecological unit) does not appear to be an important factor in a caribou's decision to use an area as a movement corridor, and is not included in the submodel.

Spatial Dependencies of Caribou Demography on Seasonal Ranges

As presently conceptualized in the CHASE framework, the main interactions between the seasonal ranges and caribou demography are (1) carrying capacity (#/ha), and (2) stage-specific mortality rate stratified by range type. Factors that influence carrying capacity are food, or the combination of food and predation. Factors that influence the mortality rates by age class are assumed to be proportional to predation risk.

Other factors or conditions that affect seasonal range demography are local disturbances caused by recreational snowmobile use (among others). For example, conditions that cause caribou to seek high-elevation winter range are also conditions that provide for some of the best recreational use of snowmobiles (MCTAC 2002) and that this use of snowmobiles is often adjacent to, or overlapping with, the same locations sought by caribou. Intense recreational use of these areas has apparently led to caribou abandoning their high-elevation winter range presumably to seek habitat of lesser value (MCTAC 2002). Inclusion of the recreational use of snowmobiles as a factor in the dynamics of high-elevation winter range is recognized as important but, despite efforts to do so, are not included successfully in the present model (CHASE 2003). They are not considered further here.

Carrying Capacity

Obtaining estimates about the number of animals that an individual range is able to support at varying levels of habitat quality is problematic mostly from a simple lack of data, information, and knowledge (CHASE 2003). Currently, the only quantitative estimates of carrying capacity are for the PLWR, and these estimates are largely expert opinion and do not have associated estimates of precision. Accordingly, for the purposes of this prototype, estimates for the other range types are generated using the following heuristics. First, CORR do not have a carrying capacity, as the population simply moves through them. Second, the HEWR and C/SR are assumed to have substantially lower carrying capacity than PLWR, and the current estimate is 20%. Given these heuristics, current estimates for carrying capacity (without predation) for each range and habitat preference class is given in Table 5.

Table 5. Estimated carrying capacity (#/ha) without predation for each seasonal range used for the prototype model. Annual variation in these estimates not shown.

Habitat Preference	HEWR	CORR	CSR	PLWR
Preferred	0.008	1000	0.008	0.04
Equivocal	0.004	1000	0.004	0.02
Avoided	0.00008	1000	0.00008	0.004



Stage-Specific Mortality

Currently, insufficient empirical data on age-specific mortality rates on each seasonal range exists to create a table of age- and range-specific survivorships from the overall survivorship data given in Section 2.2.1. A simplifying assumption is that 75% of the calf deaths occur on the calving summer range (C/SR) and the remaining 25% is equally split among the CORRs and the PLWR (i.e., no calf mortality occurs on the HEWR). Furthermore, 75% of the adult deaths appear to be associated with the movement corridors and the remainder occurs on the PLWR (i.e., no adults have been observed to die on the HEWR or the C/SR). Thus the data suggests annual survivorship estimates apportioned among the seasonal ranges as shown below in Table 6.

Table 6. Estimated annual mortality rates for each life stage on each of the seasonal range types.

Life Stage	Annual Mortality (Mean \pm SD)	Seasonal Range Mortality			
		PLWR	CORR	C/SR	HEWR
Calf	0.52 (\pm 0.07)	0.065	0.065	0.39	0
Juvenile	0 (\pm 0.15)	0	0	0	0
Yearling	0 (\pm 0.15)	0	0	0	0
Adult	0.01 (\pm 0.05)	0.0025	0.00375	0	0

Density Dependence

Most studies in long-lived ungulates assume that density dependence has a strong influence on their population dynamics. Food resources, habitat quality, predation, disease, parasites, and interspecific competition for resources can account for much of the variation on population sizes observed among years within a population or among populations within a species (Gaillard *et al.* 1998). However, the classic problem of separating out environmental factors operating in a stochastic, density-independent fashion (e.g., weather) from variation caused by the aforementioned density dependent factors is not easy in ungulates, even with long-term monitoring of marked individuals.

Reliable empirical estimates of vital rates for large herbivores are relatively uncommon, and in general life table methods do not provide means of partitioning the sources of variance among vital rates. Recruitment rates, and to a lesser extent juvenile survival, appear to be the main targets of limiting factors - density independent and density-dependent (Gaillard *et al.* 1998). Given the paucity of long-term population data for the Wolverine Herd, these problems imply that inferring when and how density dependent factors operate in response to range condition will be difficult.

Unfortunately, how density dependence is modelled has a strong influence on estimates of population persistence in response to habitat alteration (Alvarez-Buylla *et al.* 1996; Ratner *et al.* 1997; Grant and Benton 2000). Because it is likely that density dependent factors are operating at least on fecundity and likely also in part on survival rates of calves, we followed normal convention in modeling ungulate population dynamics by modeling total population sizes of the Wolverine Herd as being limited by density dependence. We assumed the predominant form of density dependence is a simple contest competition for resources (e.g., food supply) using a logistic function. Under this assumption, population growth is exponential up to K , and some individuals acquire enough resources to reproduce even if density dependence effects are strong.



If projected extinction rates of populations are low, the trajectories of ceiling models compared with logistic models show little difference, although differences will increase with increasing likelihood of extinction (Foley 1997).

Model Description

Overview

The population model is a semi-spatial stage based population model designed for efficient testing of model assumptions and analysis of sensitivity to model parameters. Rather than implement an individual based model (i.e., dividing the into discrete individuals that maintain identity like location, stage and sex), the population as a whole is allocated among risk classes within each habitat preference classes and within each seasonal range type based on estimated carrying capacity and the relative area of the landscape in each category.

The distribution of caribou within each habitat preference class is assumed to follow an ideal free distribution. Within a given seasonal range, the population is distributed into each habitat preference class based on the carrying capacity for that class, which is computed from the area for that class and a parameter specifying density at carrying capacity (Table 1). The population is first distributed in preferred habitat, then equivocal, followed by avoided. Distribution is assumed to be random within a given habitat class, such that density is uniform within a given habitat class.

Within each habitat preference class, the population is allocated into risk classes based on the proportion of that habitat preference class in each risk class. Thus, at any given time period, the population is divided into a 3 x 3 matrix representing the 9 possible habitat / risk class combinations.

Distribution in habitat/risk categories

The population is distributed following assumptions of ideal free distribution with interference. Caribou are distributed in each habitat preference class based on the relative densities in each class at carrying capacity.

$$N_i = dCC_i / \text{SUM}(dCC_i) * N_t,$$

where N_i is the number in habitat preference class i , dCC_i is the density at carrying capacity, and N_t is the total population size. In CSR, this allows some individuals into avoided even though the population is below carrying capacity in preferred and equivocal. It seems unlikely that there would be zero probability of caribou occurring in avoided habitat even under these conditions. It also allows the population to be slightly above carrying capacity in preferred and equivocal in PLWR. Since, PLWR is limiting, it seems likely that the population may be distributed at slightly higher than carrying capacity in good habitat.

Spatial Dependencies

We assume two spatial dependencies influence the overall seasonal range mortality rates: (1) density of the population relative to density at carrying capacity, and (2) the proportion of the landscape in each habitat/risk class relative to current conditions (i.e., an area weight). Seasonal range mortality can be modeled as a logistic function dependant on the ratio of the current population size to the population size at carrying capacity (pCC):

$$pCC = N_t / N_{cc},$$



where N_t is the size of the population at time t , and N_{cc} is the estimated size of the population if it were at carrying capacity for the landscape at time t .

The function is calibrated to produce the current empirical estimate of range mortality for the current population size (

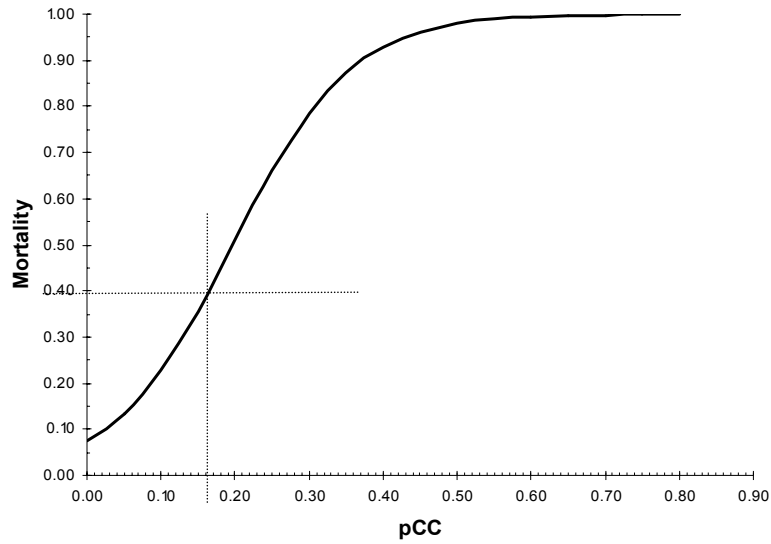


Figure 2). However, the shape of the curve is subjective.

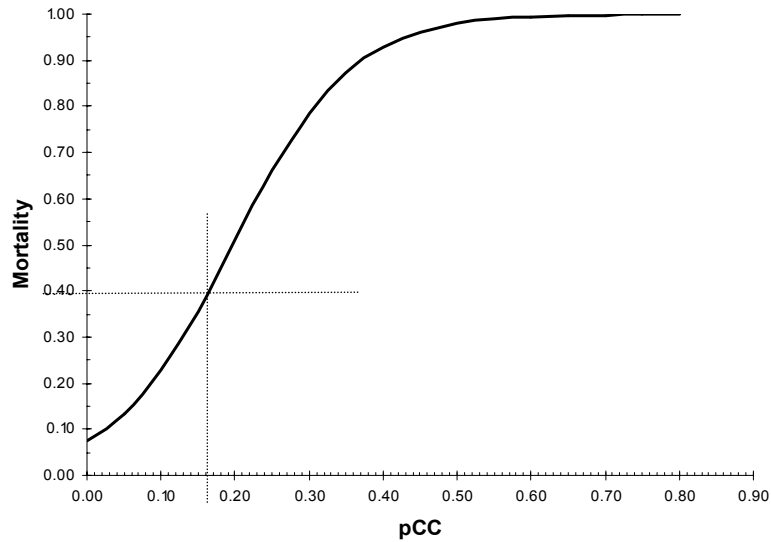


Figure 2. Example of calibrated function for estimating calf mortality as a function of current size of the population in CSR relative to size at carrying capacity. Dashed lines indicate the position on the curve corresponding to the current estimate of pCC and calf mortality in CSR. $M_r = (1 / (1 + \text{EXP}(-1*((\text{pCC} - 0.197)/0.079))))$

Table 7. Constants specifying the shape of the logistic function relating mortality to the ratio of the current population size to the size at carrying capacity for the PLWR, CSR and HEWR seasonal ranges. Values are given for stage – range combinations with estimated mortality > 0.

Life Stage	PLWR		CSR		HEWR	
	b1	b2	b1	b2	b1	b2
Calves	0.352	0.08	0.197	0.079	-	-
Yearlings	-	-	-	-	-	-
Juveniles	-	-	-	-	-	-
Adults	0.56	0.11	-	-	-	-

Density dependent mortality is further weighted by the ratio of the proportion of the landscape in each habitat-risk category in the current and initial time periods. The rationale for weighting by this ratio is based on the assumption that empirically estimated mortality rates are representative of the current configuration of the landscape. Hence, if we follow the assumptions of: (1) density dependent distribution within habitats in the range, and (2) random distribution within a given habitat type independent of predation risk, then we would expect that the cumulative mortality (as a consequence of an individuals’ position on the landscape), should be roughly equivalent to that estimated from the data. In other words, if on the current landscape we first distribute individuals into each habitat category based on the relative density at carrying capacity, and then proportionally within each risk class, then the sum of the mortality computed for each habitat-risk category should result in the same overall rate of seasonal range mortality estimated for the population.

In order to capture the relationship between the partitioned mortality rates and the area of the landscape in each habitat-risk category, we divide the proportion of the landscape in each category at a given time period t , by the proportion at $t = 0$ (i.e., at $t = 0$, all weights equal one). Assuming that the relationship between partitioned mortality and the changing proportion of landscape in each category is monotonic, these ratios can be simply applied as weights to compute the realized mortality.

A preprocessing model was developed to measure the proportion of the study area in each habitat risk class combination for each seasonal range for each decadal time step. Summarizing the spatial data in a preprocessing step provides a significant reduction in processing time for iterations of the population model run on the same projection. At the beginning of each decade, the population model reads in the previously summarized cell counts for each seasonal range and determines the area in each habitat preference class, the proportion in each risk class, and computes an area weighted mortality modifier relative to current conditions for each habitat risk class combination. Furthermore, the area weighted mortality modifier for a given year is interpolated between the values for the current and future decades; this provides a smooth transition from one decade to the next.



Spatially Distributed Realized Mortality

We compute the probability of mortality occurring in a given risk class conditional on the probability of caribou occurring in each habitat preference category.

$$P(H_{ij} | R_j) = P(H_{ij}) * P(R_j),$$

where $P(H_{ij})$ is the proportion of caribou distributed in habitat class i , risk class j , and $P(R_j)$ is the relative risk of predation for risk class j .

Mortality is then applied to each habitat-risk category by multiplying the relative conditional probability of mortality by the expected number of mortalities and the area weights:

$$eD_{ij} = (N_t * M_r) * P(H_{ij} | R_j) / \text{SUM}(P(H_{ij} | R_j)) * AW_{ij},$$

where eD_{ij} is the expected number of deaths in habitat class i , risk class j , N_t is the total number in this stage, M_r is the density dependent stage specific seasonal range mortality, $P(H_{ij} | R_j) / \text{SUM}(P(H_{ij} | R_j))$ is the relative conditional probability of mortality, and AW_{ij} is the area weight.

Because annual stage-specific mortality rates are partitioned among the four seasonal range types (Table 6), the number of mortalities occurring in each seasonal range were determined from the number of caribou in each life stage for the beginning of the year. If we were to compute mortality in each seasonal range based on the number of individuals at the beginning of the season (i.e., N at beginning of year minus the mortality in previous seasons), the within-year mortality would fall below the expected annual rates, as the rates would be applied to fewer individuals in each season.

Caribou are assumed to move through corridors at high densities and thereby experience the cumulative predation risk for the entire corridor. Because there are no limits on carrying capacity in corridors, the population cannot be distributed into habitat risk classes. Therefore, the realized mortality in corridors is computed as an area-weighted average, which represents the overall expected predation risk encountered by caribou as they move through the corridor.



Results

Interpolated Area-Weights

Figures 3 to 6 show the area weights for the landscape projection of seasonal ranges and predation risk used in the subsequent analyses. The area weights are computed as the proportion of the landscape in each habitat – risk category at each time period divided by the proportions for the current landscape. Table 8 shows the proportion of each seasonal range map in each habitat risk category for current conditions. Area weights are interpolated for each year, between proportions measured from decadal range maps to produce a smooth transition from one decade to the next. These weights are useful for examining the relative changes in composition of the landscape for a particular landscape projection scenario. For example, this particular landscape projection indicates increasing areas of high predation risk in all seasonal ranges, and increasing areas of preferred habitat in all ranges except PLWR, where preferred habitat decreases over time. In HEWR there is a large increase in the area of high predation risk in both preferred and avoided habitat within the first 3 decades, after which HEWR range quality remains relatively stable (Figure 3). In CORR there is a very large increase in avoided habitat in moderate risk class, in addition to increases in high risk areas in equivocal and avoided habitat (Figure 4). In CSR the area in high predation risk increases in all habitat preference classes steadily over all time periods (Figure 5). Whereas, in PLWR the area in high risk class decreases for preferred habitat, but increases in equivocal and avoided habitat (Figure 6).

Table 8. Proportion of seasonal ranges in each habitat-risk category for current conditions.

Range	Habitat	Predation Risk		
		High	Mod	Low
HEWR	Prf	0.0015	0.0471	0.1219
	Eqv	0.0000	0.0000	0.0000
	Avd	0.1539	0.4671	0.2085
CORR	Prf	0.0000	0.0000	0.0000
	Eqv	0.0000	0.9127	0.0000
	Avd	0.0873	0.0000	0.0000
CSR	Prf	0.0118	0.3033	0.0000
	Eqv	0.0256	0.2629	0.0000
	Avd	0.0596	0.3369	0.0000
PLWR	Prf	0.0015	0.0054	0.0003
	Eqv	0.0010	0.0024	0.0001
	Avd	0.1530	0.5064	0.3301

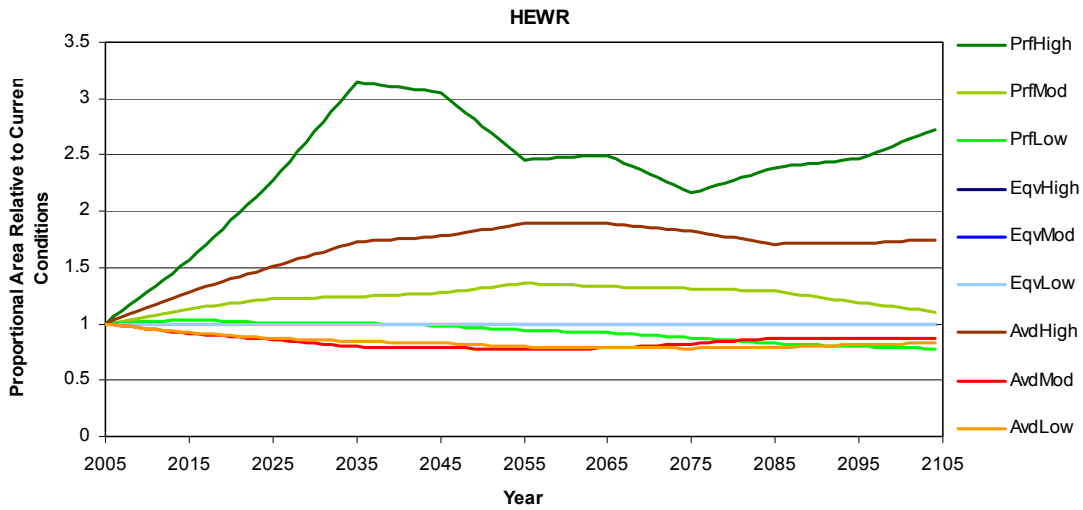


Figure 3. Interpolated area weights (proportion of landscape in each habitat-risk category computed relative to current conditions) for high elevation winter range (HEWR).

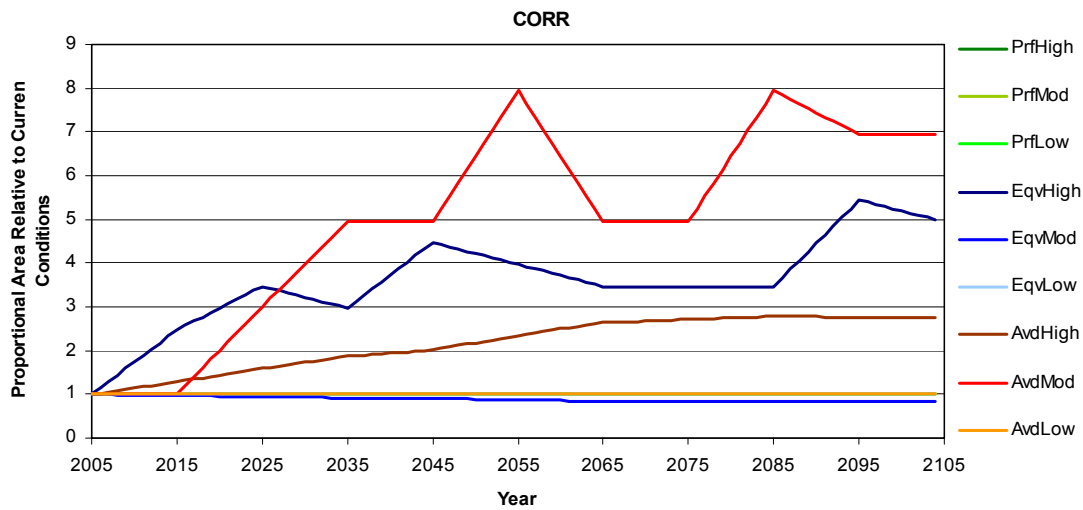


Figure 4. Interpolated area weights (proportion of landscape in each habitat-risk category computed relative to current conditions) for corridors (CORR).

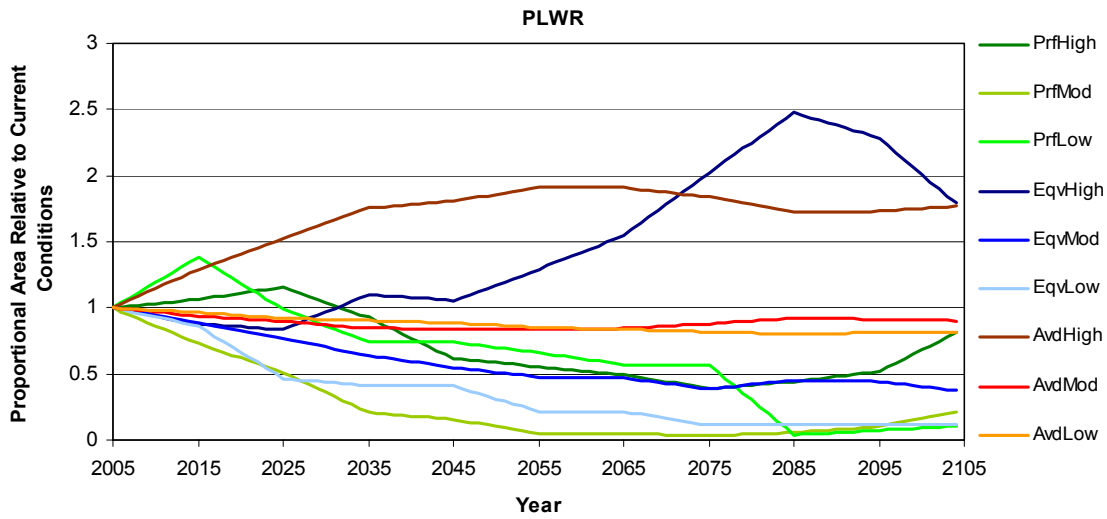


Figure 5. Interpolated area weights (proportion of landscape in each habitat-risk category computed relative to current conditions) for calving summer range (CSR).

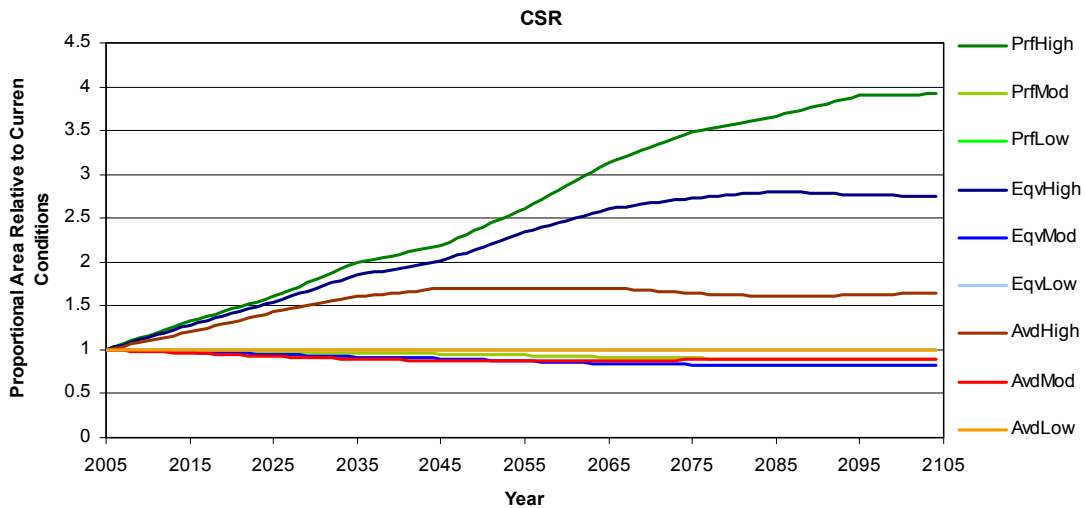


Figure 6. Interpolated area weights (proportion of landscape in each habitat-risk category computed relative to current conditions) for pine lichen winter range (PLWR).

Model Testing and Sensitivity Analysis

A series of experiments were conducted to examine the behaviour of the model to assumptions about density dependent mortality rates and variation in the empirically estimated parameter states. These included tests of (1) the effects of density dependent mortality on the model simulated on a static and dynamic landscape projection; (2) the sensitivity of the model to systematic variation in annual estimates of fecundity, calf and adult mortality; (3) sensitivity of



the model to systematic variation in estimates of carrying capacity in preferred, equivocal and avoided habitat (across all range types); (4) a series of scenarios varying proportional partitioning of annual estimates of stage-specific mortality in each seasonal range; and(5) a series of scenarios that varied the probability of predation in each predation risk category. Model simulations were also run on a landscape projected to long-term equilibrium conditions under natural disturbance.

To minimize variance between runs, and to limit variation between scenarios only to the effects of changing mean parameter rates, parameters were set to the mean value.

For the sensitivity analyses we used the parameters estimated for adult and calf mortality and fecundity and proportions in each stage for a stable population (i.e., $\lambda = 1.02$; Sutherland et al 2003). This removed the effects of declining or increasing populations on comparisons between parameter values during sensitivity testing. Starting demographic values for this steady-state condition are shown in Table 10.

Table 9. Default parameter states for sensitivity analysis.

Life Stage	Mean Annual Mortality (SD)	Mean Annual Fecundity (SD)	Initial Proportion of Population in each Stage
Calves	0.52 (0)	0	0.118
Yearlings	0 (0)	0	0.099
Juveniles	0 (0)	0.25	0.092
Adults	0.0839 (0)	0.7	0.616

1 Effects of Density Dependent Mortality on Static and Dynamic Landscape Projections.

This experiment examined the effects of running the model with density dependent mortality on both the static landscape (current conditions) and a dynamic landscape projection (i.e., the decadal time series of seasonal range maps). Unless otherwise stated, default parameter states were used.

Figure 7 compares the population trajectory for the population simulated on a dynamic landscape both with and without density dependent mortality. When simulated without density dependent mortality, the population initially grows to 600, then drops in rapid decline after 40 years. This corresponds to increases in high predation risk across all range types in the seasonal range projections (Figures 3-6). When simulated with density dependent mortality, the population increases slightly to 480 at which point density dependent mortality limits further growth. The population then undergoes steady decline over time, but the decrease is not as rapid because mortality rates decrease with lower densities in the population.

Figure 8 compares the population simulated on a static landscape both with and without density dependent mortality. When simulated without density dependent mortality, the population grows exponentially to ~2000 individuals within 100 years with a growth rate (λ) approximately equal to 1.02. This test confirms that the model is responding as expected given a set of vital rates with a specified growth rate. When simulated with density dependent mortality, the population increases slightly to ~480 and remains constant as increased recruitment is compensated for by increased mortality.

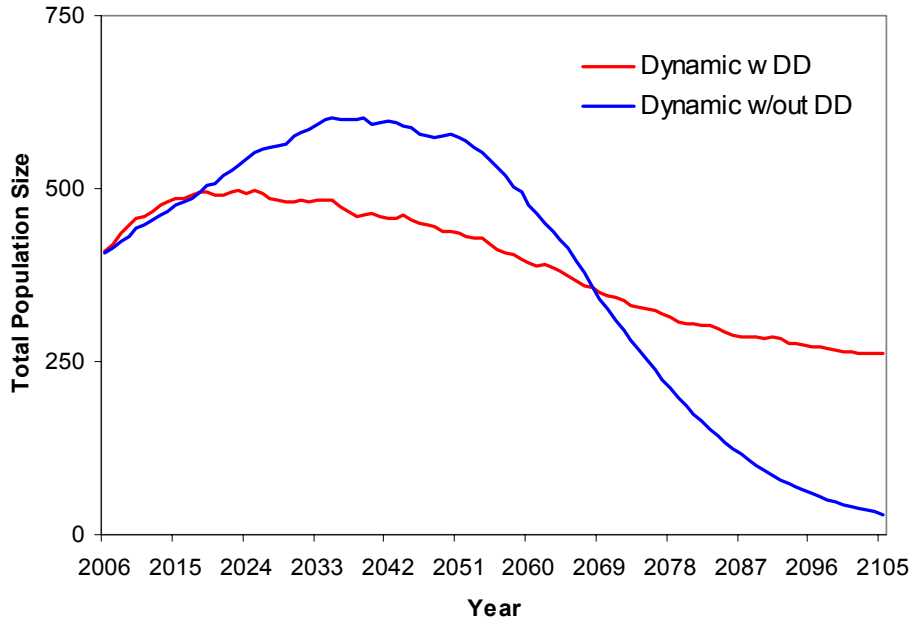


Figure 7. Population trajectory for a single population simulation on a time series of seasonal range maps both with (red line) and without (blue line) density dependent mortality.

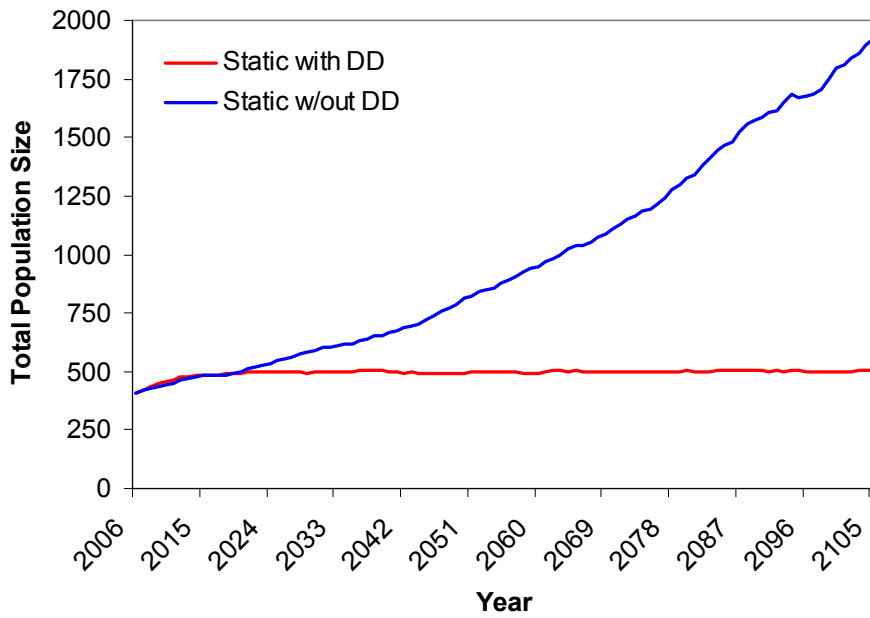


Figure 8 Population trajectory for a single population simulation on a static landscape with (red line) and without (blue line) density dependent mortality.



These tests indicate that 1) the population model is responding as expected to a vital rates with a specified growth rate; 2) density dependent mortality prevents exponential growth and under static conditions permits a stable population; 3) when simulated on the dynamic landscape projection the population declines both with and without density dependent mortality in response to increased areas of high predation risk; 4) density dependent mortality slows the rate of decrease by reducing mortality rates at lower population densities.



2 Model Sensitivity to Variation in Annual Vital Rates

This set of experiments tested the sensitivity of the model to varying rates of fecundity and mortality for model simulations both with and without density dependent mortality.

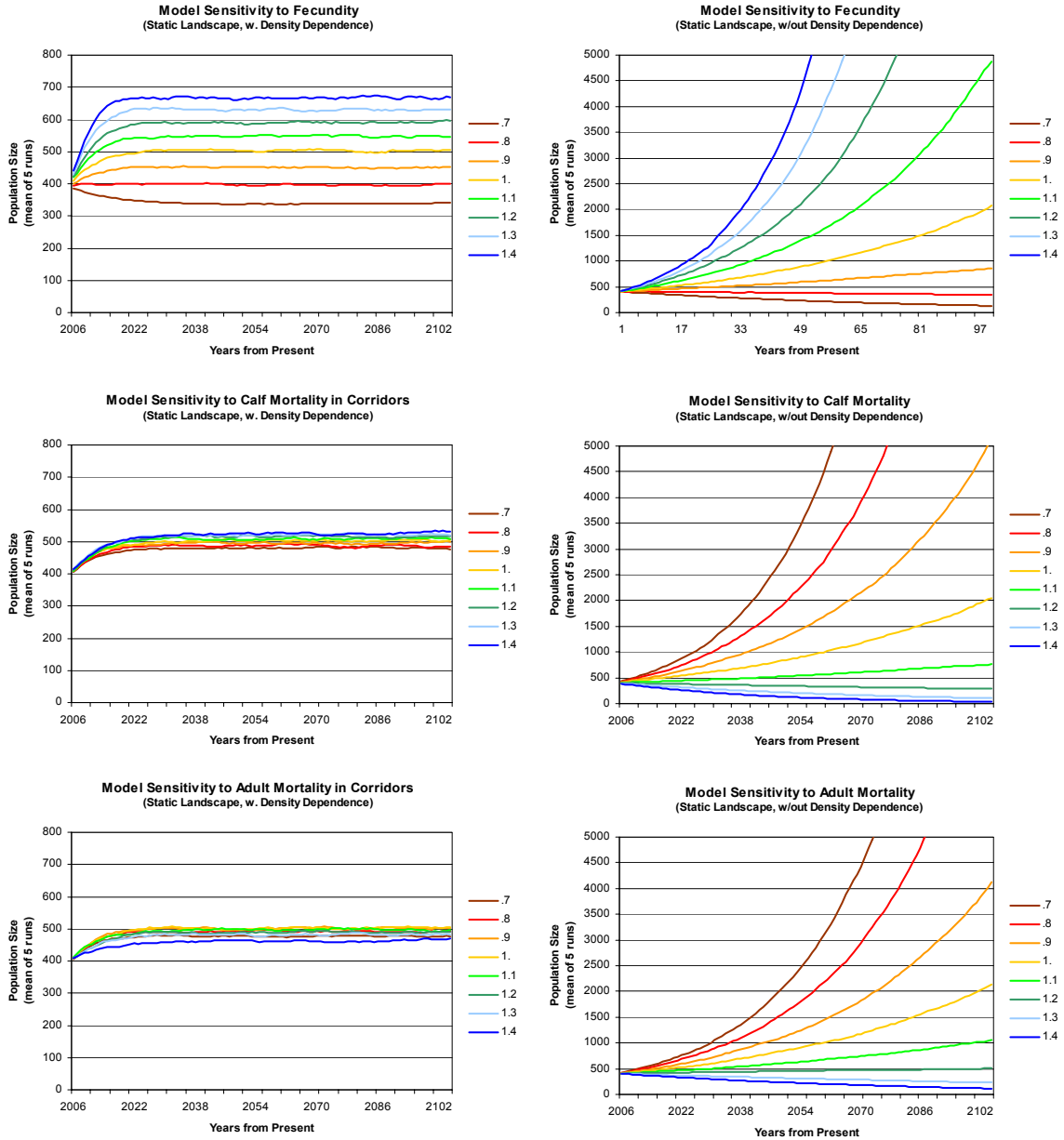


Figure 9 shows the mean trajectories of 5 simulations for each set of parameter states. A range of rates were evaluated: 70% to 140% of the default rates in 10% increments.

The model was sensitive to varying fecundity rates when simulated with density dependent mortality (**Figure 9 a**). Lowering fecundity by 30% resulted in a population decrease to 325, where it stabilizes due to decreased mortality with lower population density. At 80% fecundity the population remains at current levels of 450, and at 90% of fecundity and higher the



population increases and then stabilizes, with increases in mean population size roughly proportional to increases in fecundity. When simulated with density dependent mortality, varying rates of adult and calf mortality will only affect rates in CORR, since mortality in PLWR and CSR are dependent on population densities. Trajectories for Figure 9 c and d indicate relatively low sensitivity to variance in CORR mortality rates; with 40% increase in mortality, the population decreases by only 50 individuals. When simulated without density dependent mortality, we see exponential growth with rates of fecundity 80% above the default level. Similar patterns are evident for calf and adult mortality.

These tests indicate that under static landscape 1) the model is sensitive to varying levels of fecundity and mortality, but that density dependent mortality has a strong stabilizing effect, and quickly brings the population back to equilibrium despite increases or decreases in growth rate; 2) model sensitivity to varying levels of CORR mortality is relatively low.

3 Sensitivity of Model to Carrying Capacity

This set of experiments tested the sensitivity of the model varying levels of carrying capacity specified for each habitat preference category. For each habitat preference category, levels of carrying capacity were tested over a range of values between 80 – 130% of the default values in 10% increments. Equal scaling was applied to all range types. For each habitat class varied, the default carrying capacity rates were held constant in the other habitat types.

Figure 10 shows the mean trajectories for populations simulated with varying carrying capacities in each habitat category for simulations with and without density dependent mortality.

These tests indicate that when simulated with density dependent mortality model is most sensitive to variation in carrying capacity in preferred habitat, with little sensitivity to carrying capacity in equivocal and avoided. The model shows little sensitivity to varying carrying capacity when simulated without density dependent mortality. Generally, increasing carrying capacity in preferred habitat increased population size. This is likely because the greatest proportions of high risk area are located in equivocal and avoided habitat in CSR and PLWR (Table 8).

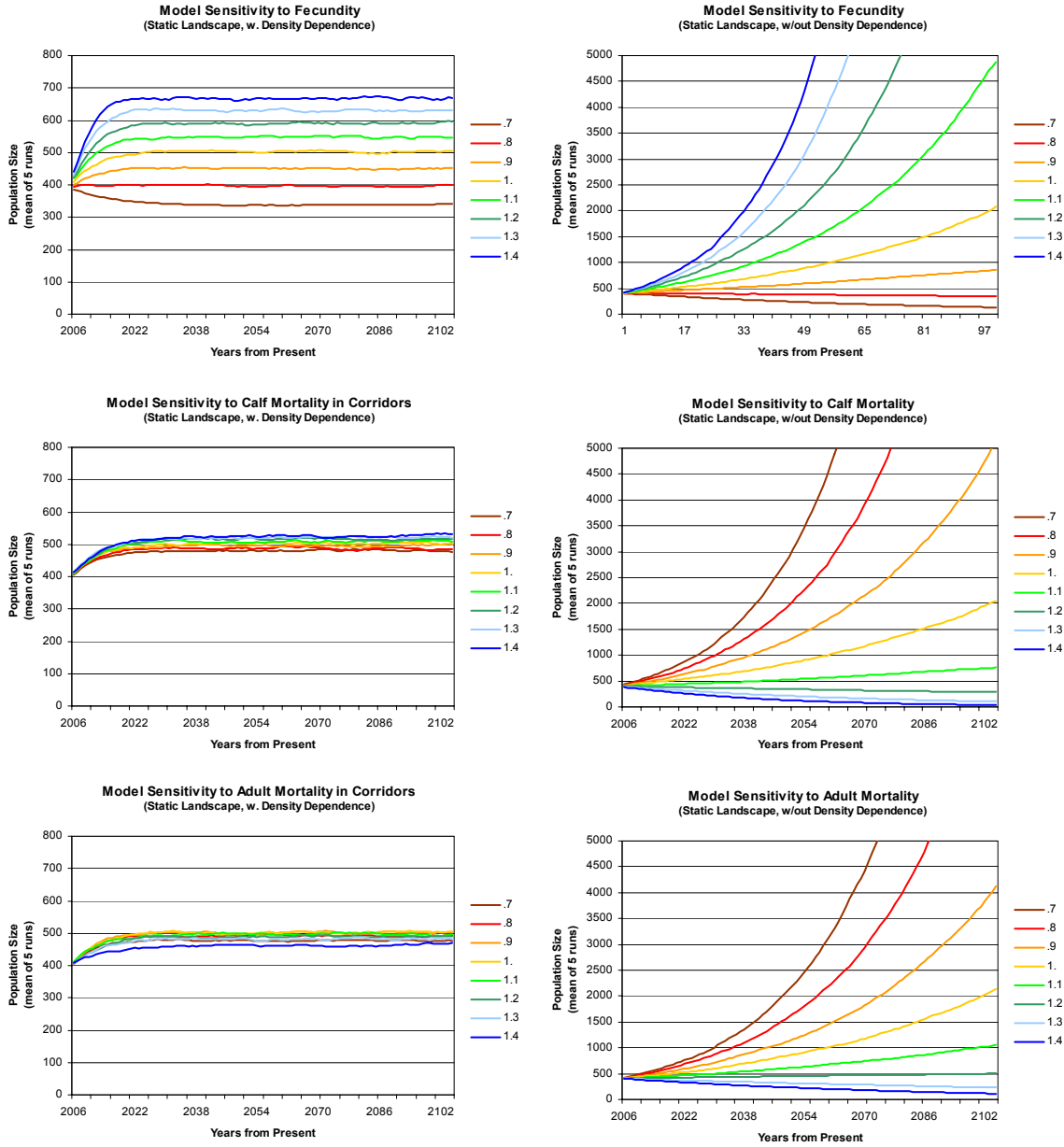


Figure 9. Model sensitivity to systematic variation in annual rates for (A,D) fecundity, (B,E) calf mortality, and (C,F) adult mortality. A static landscape was used for all model runs. Mean trajectory of the total population is shown for the model run both with (A,B,C) and without (D,E,F) density dependent mortality.

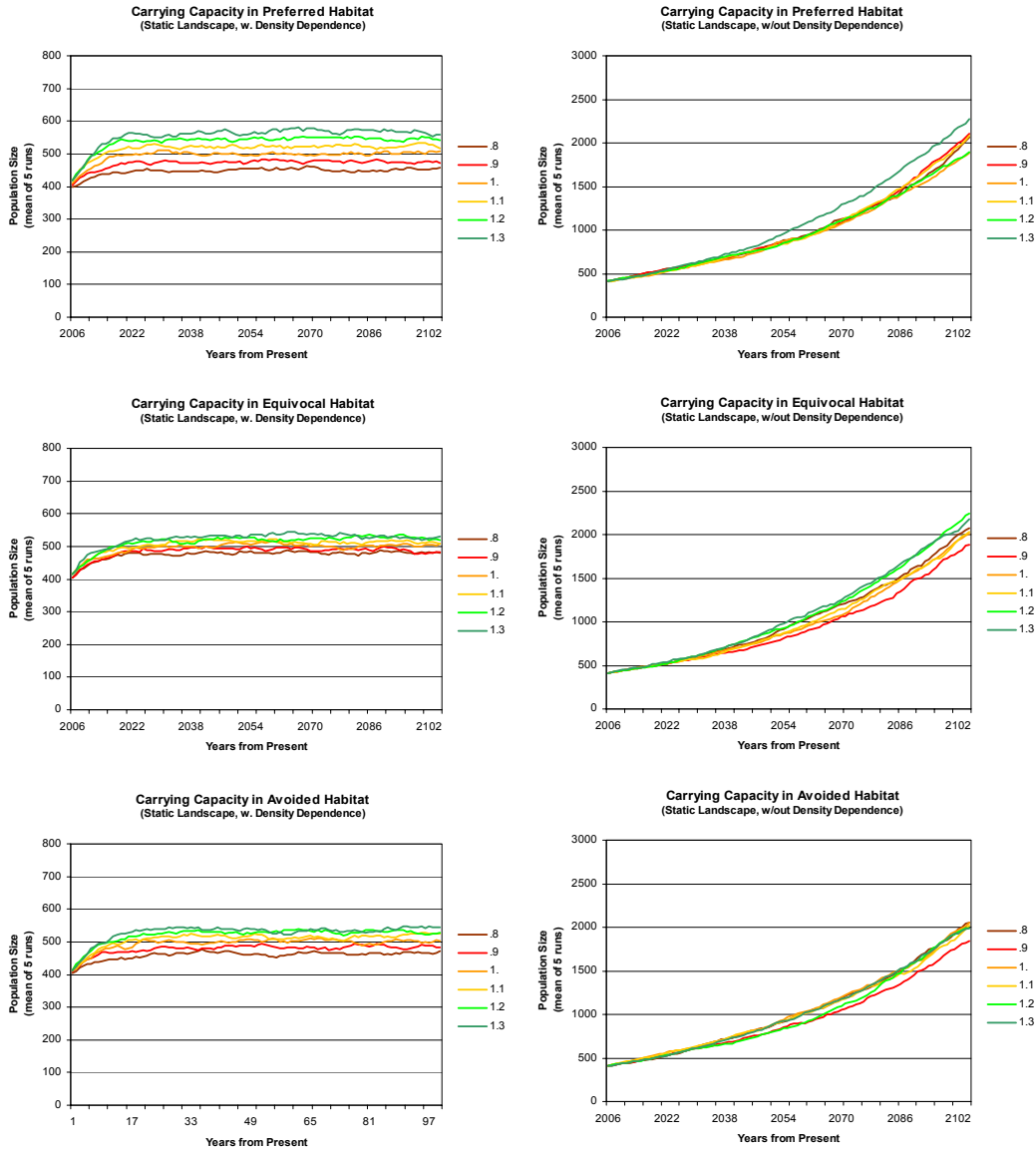


Figure 10. Model sensitivity to systematic variation in carrying capacity in preferred, equivocal and avoided habitat. A static landscape was used for all model runs. Mean trajectory of the total population is shown for the model run both with and without density dependent mortality.

4. Sensitivity of Model to the Proportion of Mortality in Each Range

This set of experiments evaluated model response to varying partitioning of mortality between seasonal ranges. Table 10 shows various changes made to the proportional allocation of mortality in each range type. Population trajectories for simulations run both with and without density dependent mortality are shown in Figure 11 and Figure 12, respectively.

**Table 10. Description of tests designed to evaluate model response to varying the proportion of mortality allocated in each seasonal range.**

	Parameter	Increase Proportion	Decrease Proportion
Test 1	Calf Mortality	Increase in CORR (0.125 to 0.375)	Decrease in CSR (0.75 to 0.5)
Test 2	Calf Mortality	Increase in CSR (0.75 to 0.8)	Decrease in CORR (0.125 to 0.075)
Test 3	Calf Mortality	Increase in PLWR (0.125 to 0.75)	Decrease in CSR (0.75 to 0.125)
Test 4	Adult Mortality	Increase in PLWR (0.25 to 0.6)	Decrease in CORR (0.375 to 0.2)
Test 5	Adult Mortality	Increase in CORR (0.375 to 0.4)	Decrease in PLWR (0.25 to 0.2)

When simulated with density dependent mortality, rates of mortality in PLWR and CSR depend on population density. Therefore, we don't expect to see large responses in the population to changes in levels of mortality for these ranges (e.g. test 3 shows little difference from default trajectory with calf mortality reallocated from CSR to PLWR). As mortality is not density dependent in CORR, we expect the model to respond to changes in the proportion of mortality allocated in movement corridors. Tests 1 and 4 show the largest population response. Test 1 doubles calf mortality in CORR, and relative to the default trajectory, the population drops from about 500 to just over 400. Test 4 decreases adult mortality in CORR from 0.375 to 0.2, and relative to the default trajectory, the population increases from 500 to about 580. When run without density dependence there is was relatively little difference in the population trajectories for all tests. This is likely because the overall annual mortality rates do not change, just the allocation of mortality between ranges. Hence, we would expect to see the same overall levels of mortality for all tests.

These tests indicate that 1) when simulated without density dependent mortality, the model is not very sensitive to portioning of mortality between seasonal ranges because the same overall rates of mortality are being applied; 2) when simulated with density dependent mortality, the model is sensitive only to reallocation of mortality in CORR; and 3) the model is more sensitive to increases in CORR mortality than decreases, in part because default proportion of mortality in CORR is relatively low.

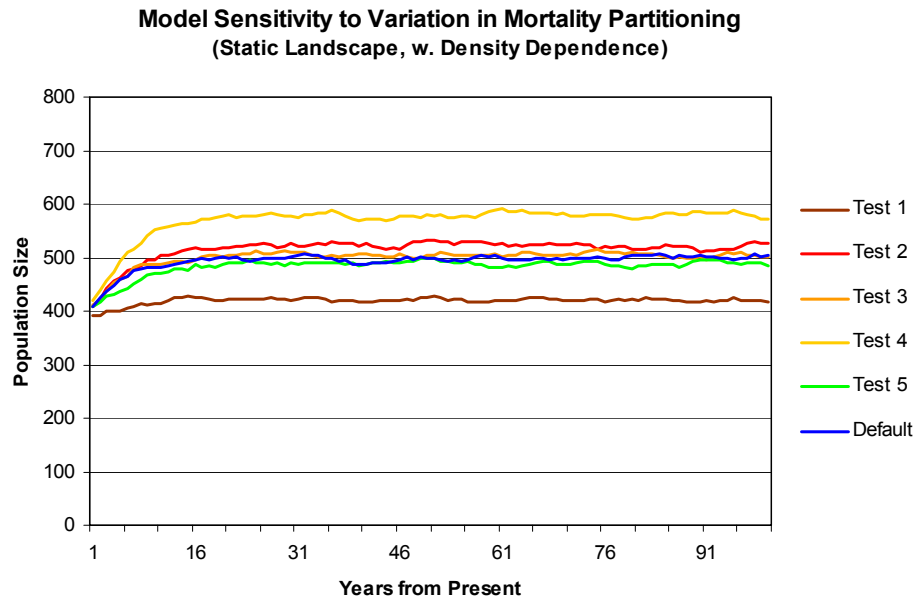


Figure 11. Simulated population trajectories with variations in proportional allocation of mortality among range types (see Table 10 for test descriptions). Model run with density dependent mortality on a static landscape. The trajectory for the default parameter states is provided for reference.

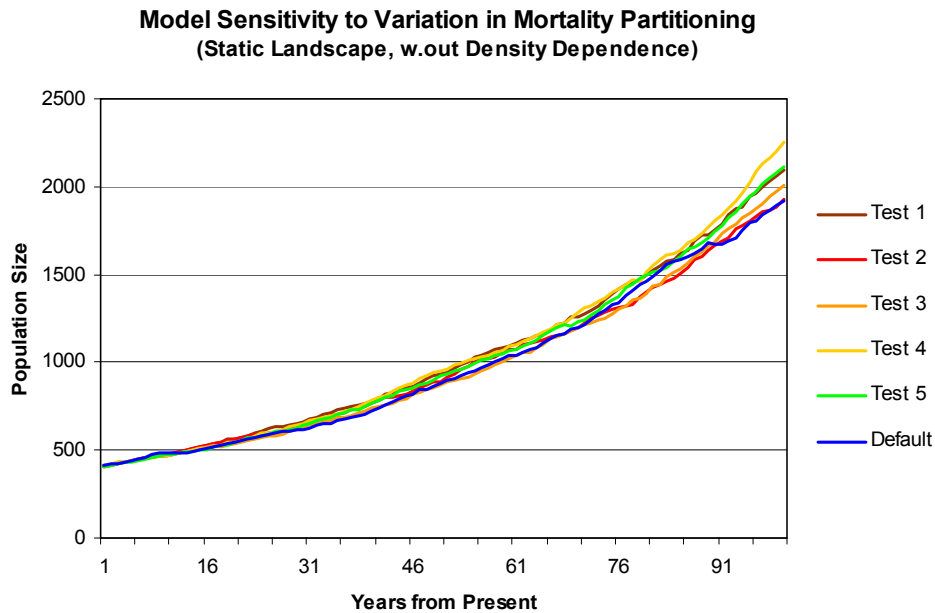


Figure 12. Simulated population trajectories with variations in proportional allocation of mortality among range types (see Table 9 for test descriptions). Model run with density dependent mortality on a static landscape.



5. Sensitivity of Model to Predation Risk

This set of tests evaluates response of the model to variation in the probability of mortality occurring in each predation risk class (high, moderate, low). Tests were run on a static landscape, both with and with out density dependent mortality. Parameter values used in each test are shown in Table 11. Population trajectories for each test are shown in Figure 13 and Figure 16.

Table 11. Values for the proportion of mortality occurring in each predation risk class

	Proportion of Mortality in Each Risk Class		
	High	Moderate	Low
Test 1	0.33	0.33	0.33
Test 2	1	0	0
Test 3	0	1	0
Test 4	0	0	1
Test 5	1	1	1

When simulated with density dependent mortality, there was relatively little difference from default trajectory with equal distribution of predation risk (test 1). With 100% mortality in high risk, the population doubles; remains unchanged with 100% mortality in moderate risk and grows rapidly and exponentially with 100% mortality in low risk. Interestingly, at a population size of ~800,000 the population stabilizes under density dependent mortality (Figure 14).

These tests indicate that for simulations both with and without density dependence, 1) assigning 100% mortality to low risk class results in rapid and exponential growth, likely because there is very little area in low risk in PLWR, and there is currently no mortality associated with HEWR (Table 8); and 2) assigning 100% mortality in high risk areas doubles the population size, but growth stabilizes because there is still significant areas in high risk for all range types (Table 8).

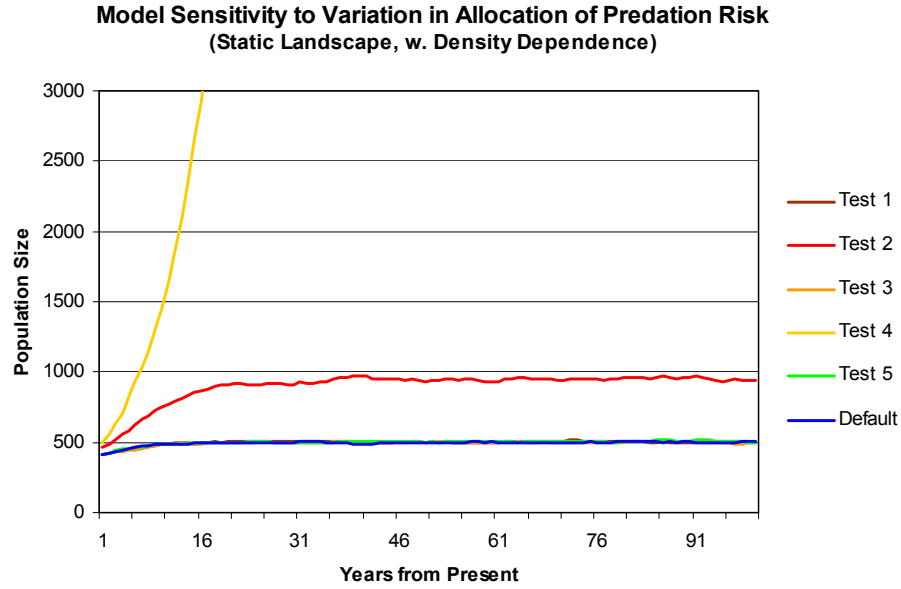


Figure 13. Simulated population trajectories with variations in proportional allocation of predation risk among risk classes (see Table 11 for test descriptions). Model run with density dependent mortality on a static landscape.

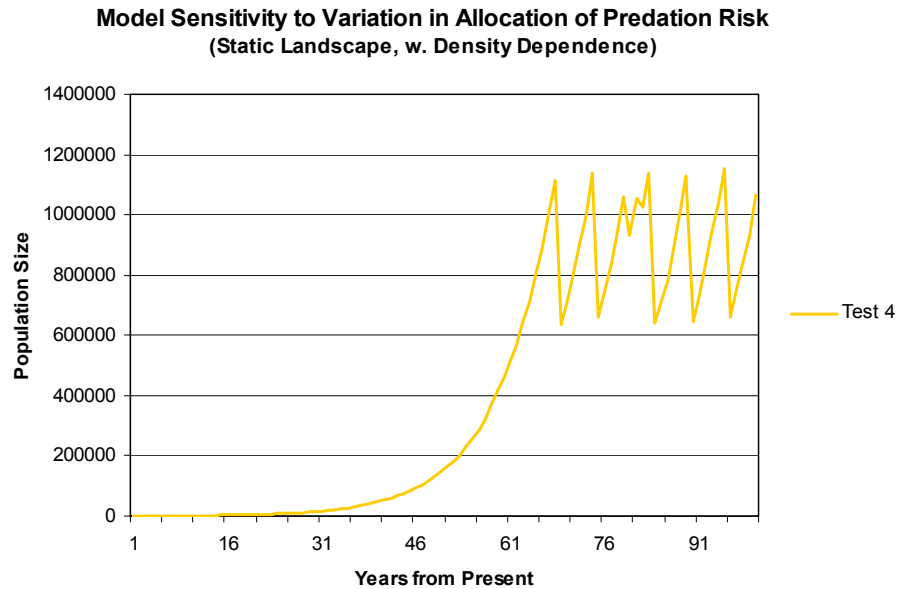


Figure 14. Simulated population trajectory for test 4 with y-axis scale adjusted to maximum.

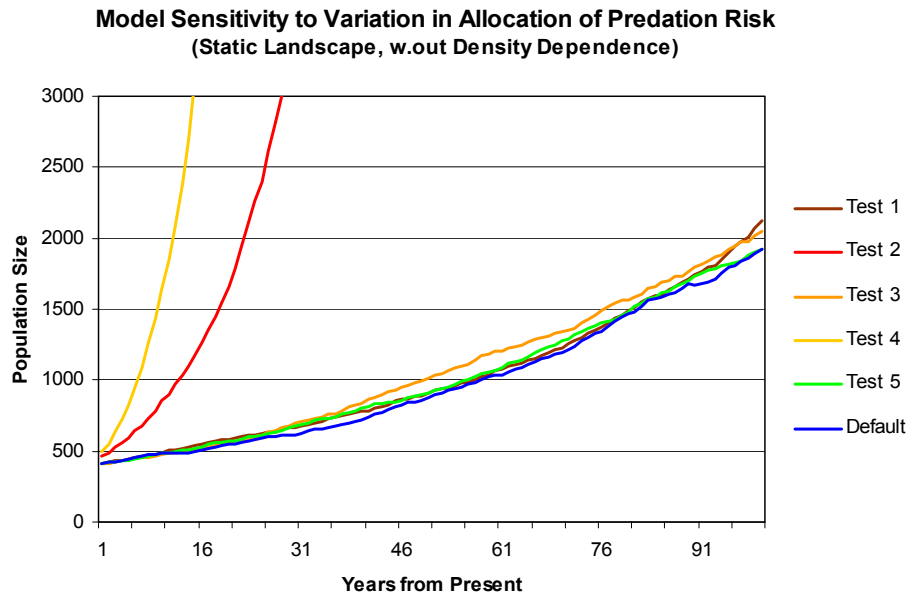


Figure 15. Simulated population trajectories with variations in proportional allocation of predation risk among risk classes (see Table 10 for test descriptions). Model run without density dependent mortality on a static landscape.

6 Natural Disturbance Scenario

This scenario was designed to evaluate the response of the simulated population to a long-term equilibrium landscape (LTE) projected under natural disturbance as the sole disturbance agent. As before, the area-weights were computed as the ratio of the proportion of the LTE landscape in each habitat-risk category to proportions measured for the current landscape (Table 12).

Table 12. Area-weights for long-term equilibrium landscape computed relative to current conditions.

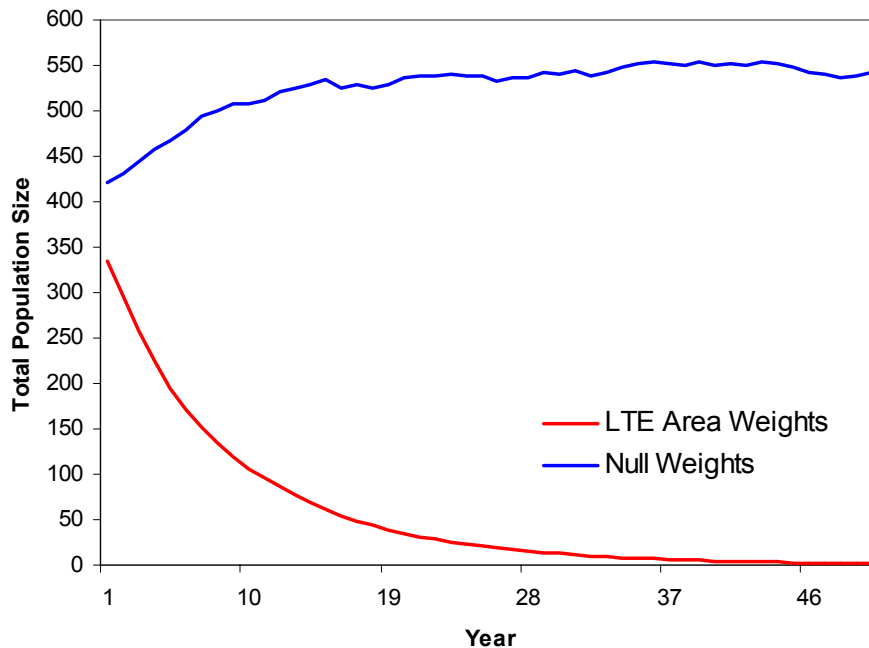
PLWR LTE Area Weights	Predation Risk		
	High	Mod	Low
Preferred	1.23	0.23	0.019
Equivocal	2.20	0.43	0.23
Avoided	2.17	0.81	0.76



CSR LTE Area			
Weights	Predation Risk		
Habitat Preference	High	Mod	Low
Preferred	11.67	0.56	1
Equivocal	5.71	0.46	1
Avoided	3.39	0.67	1
CORR LTE Area			
Weights	Predation Risk		
Habitat Preference	High	Mod	Low
Preferred	1	1	1
Equivocal	0.5	0.66	1
Avoided	4.53	0	1
HEWR LTE Area			
Weights	Predation Risk		
Habitat Preference	High	Mod	Low
Preferred	0.0066	0.005	0.006
Equivocal	14.85	74.63	68.81
Avoided	2.17	0.87	1.17

The population was simulated using density dependent mortality and the static LTE landscape. Two simulations were run: 1) with the area-weights computed relative to current conditions, and 2) with a null set of area-weights all set to 1. The resulting population trajectories are shown in Figure 16.

Figure 16. Simulated population trajectories on the landscape equilibrated to natural disturbances for scenario with area weights computed relative to current conditions (blue line) and a scenario with null weights with values set equal to one. Simulated with density dependent mortality.



Relative to current conditions, the LTE landscape has a very large increase in area of high predation risk in the CSR range; a substantial decrease in moderate risk area in PLWR and CSR; and a substantial decrease in area of low predation risk in PLWR (Table 12). The area of preferred habitat in HEWR drops substantially, and with a relatively large increase in the area in equivocal habitat (Table 11). Clearly, the large increase in area of high predation risk in all habitat classes results in a strongly declining population when simulated using the relative area weights (Figure 16). However, when run with the null set of weights, the population grows to ~530 individuals and remains stable, suggesting an increase in the carrying capacity of the landscape (independent of predation risk).

The extreme response of the population to large area-weights in the CSR range of the LTE landscape suggest that the relationship between mortality and relative area of habitat in each habitat-risk category is non-linear. With large area-weights, the realized mortality for a given habitat-risk category will reach 100% mortality.

These tests indicate that (1) the model is very sensitive to relatively large and sudden shifts in the area in each habitat- predation risk category; and (2) this version of the LTE landscape is not likely to support a caribou population under current assumptions of mortality, predation risk and density dependence.



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