

## Population Viability of Barren-Ground Grizzly Bears in Nunavut and the Northwest Territories

PHILIP D. McLOUGHLIN,<sup>1,2</sup> MITCHELL K. TAYLOR,<sup>3</sup> H. DEAN CLUFF,<sup>4</sup> ROBERT J. GAU,<sup>4</sup> ROBERT MULDER,<sup>4</sup> RAY L. CASE<sup>4</sup> and FRANÇOIS MESSIER<sup>1</sup>

(Received 28 March 2002; accepted in revised form 3 September 2002)

**ABSTRACT.** We modelled probabilities of population decline as a function of annual kill for a population of barren-ground grizzly bears (*Ursus arctos*) inhabiting Nunavut and the Northwest Territories, Canada. Our results suggest that the population is at risk of decline, especially if annual removal rates increase from the 42-year mean of 13.4 bears per year. Adding six bears to the mean annual kill results in a greater than 40% chance of a decrease by one-quarter in population size over the next 50 years, compared to a 10% chance with the current level of human-caused mortality. Additional mortalities may result from increased problem behaviour by bears at mine sites or hunt and exploration camps, given recent increases in human activity in the region, and may already be present as unreported mortality. We believe any increase in current harvest quotas would considerably lessen conservation prospects for the population.

**Key words:** Arctic, demography, grizzly bear, harvest, Northwest Territories, Nunavut, population viability, PVA, *Ursus arctos*

**RÉSUMÉ.** On a simulé les probabilités de baisse de la population en fonction du prélèvement annuel dans le cadre de la chasse pour une population de grizzlis de la toundra (*Ursus arctos*) habitant le Nunavut et les Territoires du Nord-Ouest, au Canada. Nos résultats suggèrent que la population risque de décliner, surtout si les taux de prélèvement augmentent par rapport à la moyenne établie sur 42 ans qui est de 13,4 ours par an. Le fait d'ajouter 6 ours au prélèvement de chasse annuel augmente à plus de 40 % le risque que la population décline d'un quart au cours des prochains 50 ans, par rapport à 10 % dans le cas du niveau actuel de mortalité provoquée par les humains. Vu l'augmentation récente de l'activité anthropique dans la région, d'autres individus pourraient être abattus à cause du nombre croissant de comportements problématiques des ours résidant à des sites miniers et à des campements d'exploration, et il est possible que ce phénomène existe déjà mais que les morts ne soient pas rapportées. Notre opinion est que toute augmentation des quotas actuels de prélèvement réduirait considérablement les perspectives de conservation pour la population.

**Mots clés:** Arctique, démographie, ours grizzli, prélèvement, Territoires du Nord-Ouest, Nunavut, viabilité de la population, analyse de la viabilité de la population, *Ursus arctos*

Traduit pour la revue *Arctic* par Nésida Loyer.

### INTRODUCTION

The life history traits of grizzly bears (*Ursus arctos*) generally limit the resilience of populations threatened by human disturbance. Late age at maturity, small litter sizes, and long interbirth intervals maintain low intrinsic rates of increase for the species. Because of this, all grizzly bear populations in Canada are considered to be of 'special concern' to the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (2000). However, grizzly bears show great diversity in life history strategy (Ferguson and McLoughlin, 2000), and we can predict that not all

populations of grizzly bears will be equally resilient (or susceptible) to anthropogenic disturbances.

Barren-ground grizzly bears inhabiting Canada's central Arctic (Fig. 1) may be at particular risk of population decline. They are located near the northernmost and easternmost extent of grizzly bear range in North America, and the population is characterized by relatively low density and small bears that live in areas of low productivity and high seasonality (Ferguson and McLoughlin, 2000; McLoughlin et al., 2000). Consequently, we can expect a generally low rate of reproduction relative to other grizzly bear populations, resulting from delayed age at first parturition, longer birth

<sup>1</sup> Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan S7N 5E2, Canada

<sup>2</sup> Present address: Department of Biological Sciences, CW-405 Biological Sciences Centre, University of Alberta, Edmonton, Alberta T6G 2E9, Canada; pdm5@ualberta.ca

<sup>3</sup> P.O. Box 1000, Department of Sustainable Development, Government of Nunavut, Iqaluit, Nunavut X0A 0H0, Canada

<sup>4</sup> Department of Resources, Wildlife, and Economic Development, Government of the Northwest Territories, #600, 5102-50 Avenue, Yellowknife, Northwest Territories X1A 3S8, Canada

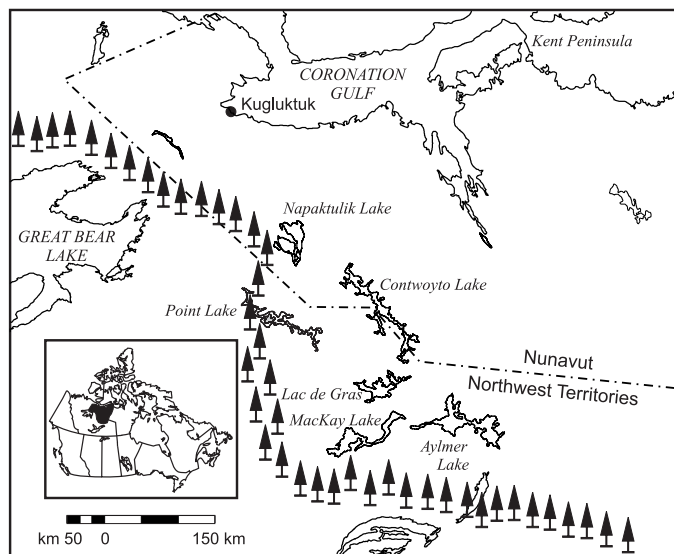


FIG. 1. The study area (shaded region) in Canada's central Arctic. The tree line indicates the northernmost extent of coniferous forest.

and reproductive intervals, and smaller litter sizes. Of all grizzly bear populations, barren-ground populations may experience the most pronounced effect on their viability from direct mortality associated with human activity.

In 1995, to address concerns about the potential effects of increasing human activity on barren-ground grizzly bears inhabiting Canada's central Arctic, the Government of the Northwest Territories and the University of Saskatchewan initiated a multi-faceted research program into the ecology of barren-ground grizzly bears (e.g., Gau, 1998; McLoughlin, 2000; McLoughlin et al., 1999, 2002). As part of this program, we described the demography of grizzly bears in the region (McLoughlin and Messier, 2001). Here we model population viability of barren-ground grizzly bears in Nunavut and the Northwest Territories.

## METHODS

### Study Area

The study area, located in Canada's central Arctic, encompassed approximately 235 000 km<sup>2</sup> of Low Arctic tundra in mainland Nunavut and the Northwest Territories (Fig. 1). McLoughlin et al. (2002) provide a detailed description of the landscape typical of grizzly bear range in the Low Arctic.

### Animals and Vital Rates

From May 1988 to June 1999, capture crews immobilized grizzly bears on at least 330 occasions to obtain information on vital rates of the population. Since some bears were immobilized more than once, the total number immobilized was 283 animals. Reproductive histories of grizzly bears were determined by visual relocations of

radio-collared animals in spring of each year; survival was determined by monitoring activity sensors on collars and via annual visual relocations (McLoughlin and Messier, 2001). For the period 1988–91, 15 females were monitored in the Kugluktuk region of the study area (Case and Buckland, 1998). From 1995 to 1998, 81 bears (38 adult females, 4 subadult females, 35 adult males, and 4 subadult males) were monitored throughout the whole of the study area, including the Kugluktuk region, which has a high rate of interchange of individuals with the central and eastern portions of the study area (McLoughlin, 2000). Vital rates (survival rates and reproductive data) presented in McLoughlin and Messier (2001) form the basis of analyses presented here.

### Modeling Population Viability

Population viability analysis (PVA) uses measures of vital rates for populations and effects of demographic and environmental stochasticity on population growth to evaluate probabilities of population persistence for a specified period of time (Boyce, 1992). The usual approach for estimating persistence is to develop a probability distribution for the number of years before population models for a species "go extinct," or fall below a specified threshold. The percentage of area under this distribution where the population persists beyond a specified time period is equated to persistence. For a review of PVA, including its merits and shortfalls, we refer the reader to White (2000).

Here we use a Windows-compatible program named RISKMAN (see, e.g., Eastridge and Clark, 2001) to model population viability for grizzly bears in the central Canadian Arctic. The model is available at no cost from M.K. Taylor upon written request. RISKMAN differs from other simulation models in several ways. First, it provides an option for accurately modelling the population dynamics of species with multi-year reproduction schedules, such as grizzly bears (Taylor et al., 1987). Second, RISKMAN allows sex- and age-specific harvests to occur that take into account differential sex and age class vulnerability to harvest and differential sex and age class selectivity by hunters. Third, the program provides a stochastic option that uses the variance of input parameters and the structure identified by the simulation options that are selected. Monte Carlo techniques are used to generate a distribution of results, and RISKMAN uses this distribution to estimate the variance of summary parameters (e.g., population size at a future time, population growth rate, and proportion of runs that result in a population decline set at a pre-determined level by the user). The model incorporates individual heterogeneity by relying on a life table approach (Caughley, 1977) rather than a Leslie matrix (Leslie, 1945) to model population dynamics. Individuals simultaneously survive and reproduce with the Leslie matrix approach, whereas the life table approach has the females first survive, and then reproduce (Taylor and Carley, 1988). Having females survive first enables heterogeneity

TABLE 1. Natural survival rates (mean, SE) calculated using methods of Trent and Rongstad (1974) and used to develop population models in RISKMAN (originally presented in McLoughlin and Messier, 2001). Parameters include survival of cubs ( $S_c$ ), yearlings ( $S_y$ ), subadult females ( $S_{sf}$ ), subadult males ( $S_{sm}$ ), adult females ( $S_{af}$ ), and adult males ( $S_{am}$ ). Two rates are presented: (A) for confirmed mortalities only and (B) for confirmed + unconfirmed mortalities (incorporating 7 missing radios into survival estimates).

	(A)		(B)	
	Confirmed Mortalities Only		Unconfirmed Mortalities Included	
	Mean	SE	Mean	SE
$S_c$	0.737	0.060	0.737	0.060
$S_y$	0.683	0.074	0.683	0.074
$S_{sf}$	0.831	0.148	0.814	0.131
$S_{sm}$	0.833	0.150	0.816	0.133
$S_{af}$	0.979	0.012	0.945	0.019
$S_{am}$	0.983	0.017	0.948	0.029

in female survival to influence reproduction for any given year, which may be important for accuracy in models of population viability (White, 2000).

#### Model Input

Input required to run our PVA was obtained from calculations and tables presented in McLoughlin and Messier (2001) and reproduced here in Table 1. We calculated the proportion of females with new litters having one, two, or three cubs-of-the-year in their litters to be 0.17, 0.46, and 0.37, respectively. The mean proportion of females that were available for mating in the previous year (i.e., they had no cubs, or cubs that were at least two years old) and then gave birth to a litter was 0.20 (SE = 0.11) for females aged 5–7 years, and 0.60 (SE = 0.08) for females aged 8 years or older. In our simulations, we used a minimum age of reproduction of five years, and a maximum of 25 years. Maximum age was set at 30 years.

Finite rate of population increase is not an input required by RISKMAN, as the program itself calculates it. Although there are provisions to model density-dependent effects in RISKMAN, we had no data to model such effects here (McLellan, 1994; Boyce, 1995; Mills et al., 1996; Wielgus, 2002).

The mean removal rate of bears inhabiting the study area, calculated as 13.4 bears per year, reflects kills that are for sport, subsistence, and the protection of life and property. Estimates of unknown, illegal kills are not included in this estimate. We assume here that the harvest in each year will be composed of the relative sex/age strata depicted in McLoughlin and Messier (2001) and Government of the Northwest Territories harvest records, 1958–2000 (data on file). We used an initial population estimate of 800 bears, which was an extrapolation from counts of uniquely identified (tagged and untagged) bears observed for the central portion of the study area (McLoughlin and Messier,

2001). We ran simulations using SE of population size of 300, 200, and 150 to reflect our uncertainty about this mean, and to appreciate the sensitivity of our model outcomes to sampling error in initial population size.

We were unable to separate environmental stochastic effects in vital rates from measurement errors for all rates, as annual variability in rates for cubs-of-the-year, yearlings, and subadults was unavailable. This likely had the effect of generating conservative probabilities of persistence (White, 2000; M. Boyce, University of Alberta, pers. comm. 2002). Effects of catastrophes were not incorporated into models (Ewans et al., 1987), nor were potentially detrimental effects of inbreeding (Lacy, 1993; Lindenmayer et al., 1995). We assumed annual random deviates of parameter values were independent for lack of data on temporal variability, although it is possible and perhaps likely that parameters were correlated (White, 2000).

#### Models

We ran RISKMAN models to evaluate the potential risk that harvest could generate a decline in the grizzly bear population. We estimated the probability of the grizzly bear population's declining by 25%, 50%, and 75% of the current population size over a specified time interval of 50 years from the present. To examine the risks of increasing the current harvest, or to account for possible risks of unreported illegal harvest, we ran simulations with the mean annual harvest rate increased by six bears annually. This higher harvest level reflects recent requests by communities in the study area to increase the annual sport hunt of grizzly bears from 10 to 16 animals. To account for uncertainty in our survival data, we ran simulations that decreased estimates of rate of increase by including bears that went missing during our monitoring program as unconfirmed mortalities.

RISKMAN is designed to provide Monte Carlo estimates of the uncertainty of simulation results using the variance of input parameters. Our rationale for model structure and approach to variance is summarized in Taylor et al. (2001). We ran 2800 stochastic simulations for each year of a simulation to provide a distribution of model outcomes (i.e., population numbers at survey time) from which risks of population declines were estimated.

## RESULTS

The number of simulation runs leading to set thresholds of population decline was sensitive to the SE of the initial population size (Figs. 2–4). However, we believed SE = 200 to best describe the SE associated with our estimate of population size (Fig. 3). Translated into a 95% confidence interval, a SE of 200 would result in an interval of approximately 400–1200 around our initial population size of 800 bears.

Using the highest estimates available for natural survival rates and a population SE = 200, we estimated the

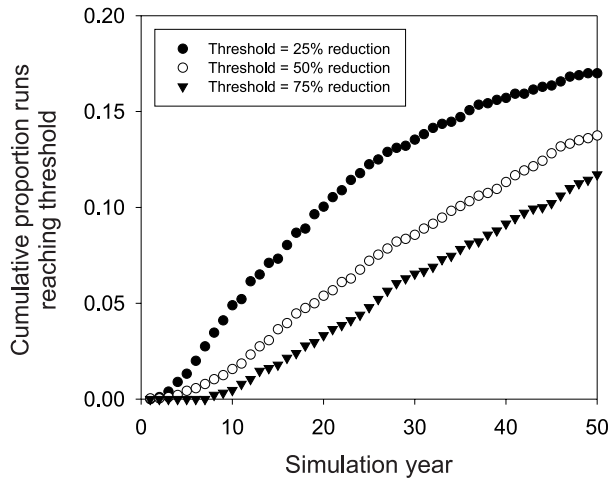


FIG. 2. Projections of population decrease over 50 years, based on initial population size of 800 ( $\pm$  300 SE) bears. Symbols show the cumulative proportion of RISKMAN population simulation runs projected to reach reductions of 25% (●), 50% (○), and 75% (▼) over time. Simulations were performed using the highest survival rates available and a removal rate of 13.4 bears per year.

probabilities of the initial population’s declining by 25% (0.10), 50% (0.07), and 75% (0.05) over the next 50 years (Fig. 3). These results were based on past harvest records detailing the selectivity/vulnerability of different age strata and a mean removal from the population of 13.4 bears each year through sport hunting, subsistence hunting, and kills in defence of life or property. These results can be regarded as the “best case” and also the most likely scenario, given our current understanding of grizzly bears in the region.

Increasing the kill by six bears per year dramatically increased risks of population decline. With a mean removal of 19.4 bears per year, we estimated that the probabilities of the current population’s declining by 25%, 50%, and 75% over the next 50 years would be 0.42, 0.32, and 0.18, respectively (Fig. 5).

By including missing bears for which no collar was recovered in McLoughlin and Messier (2001) as unconfirmed natural mortalities in the simulations, and retaining a mean of 13.4 bears/year removed from the population by the harvest, we estimated that the probabilities of the current population’s declining by 25%, 50%, and 75% over the next 50 years would be 0.99, 0.99, and 0.98, respectively (Fig. 6). We caution that this situation probably underestimates natural survival, but we have included it here for completeness. Six of seven missing adults disappeared two years after their initial capture and beyond the lifespan of their satellite radio-collars, likely impeding our ability to include them in the spring 1997 census (McLoughlin and Messier, 2001).

DISCUSSION

Although we believe the population to be currently stable or slightly increasing ( $\lambda = 1.033$ , 95% C.I. 1.008–1.064; McLoughlin and Messier, 2001), our results

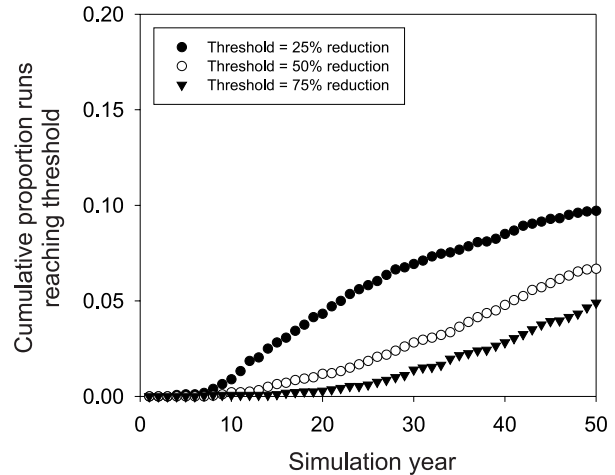


FIG. 3. Projections of population decrease over 50 years, based on initial population size of 800 bears ( $\pm$  200 SE) bears (details as in Fig. 2).

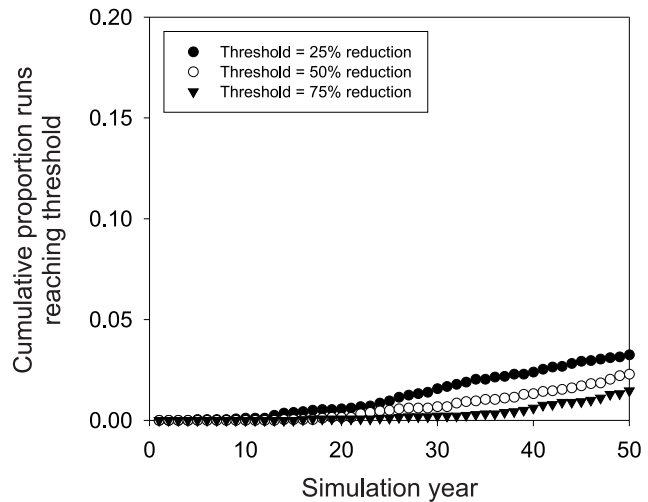


FIG. 4. Projections of population decrease over 50 years, based on initial population size of 800 bears ( $\pm$  150 SE) bears (details as in Fig. 2).

suggest that the population is at risk of decline, especially if the annual kill is increased from the mean of 13.4 bears per year. Even if we ignore missing radios in our study as possible deaths, our risk analyses suggest that the population of grizzly bears in the central Arctic has the potential to decrease substantially within our lifetimes. Adding only six animals to the mean removal rate produces a greater than 40% chance that the population will decrease by one-quarter over the next 50 years, up from a 10% chance with current estimates of kill rate. These six bears could easily come from increased problem activity at hunting and exploration camps or mine sites, and they may already be present as unreported mortality. In this study, we retrieved from the field three discarded satellite radio-collars, all in excellent condition but opened, with all fastening nuts removed. On no other occasions did we find collars with any fastening nuts loose or missing, even those that had suffered considerable abuse. We suspect the bears that wore these collars were illegally harvested; however, these

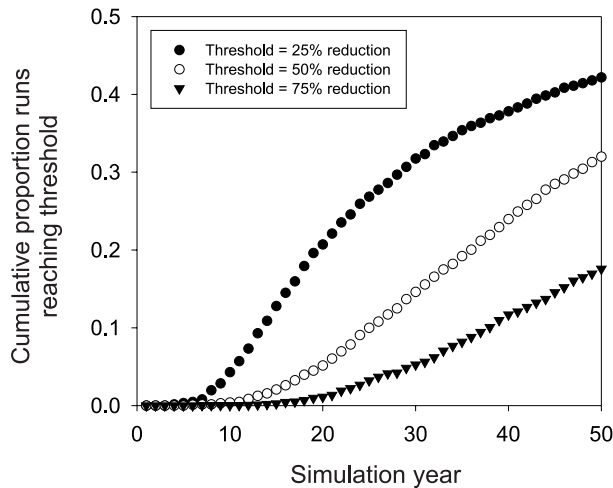


FIG. 5. Projection of population decrease over 50 years, based on an increased harvest of 19.4 bears per year from initial population of 800 ( $\pm 200$  SE) bears (details as in Fig. 3). Increasing the mean harvest rate by 5 bears per year dramatically increases the risks of population decline.

harvests were not included in the harvest records used in our RISKMAN analyses (harvest records from 1958–2000 include only two illegal harvests; data on file).

We consider grizzly bears in the central Arctic to be in danger of experiencing population decline, especially in the context of increasing human activity in the study area. Industrial development in the region is proceeding at a rapid pace, primarily because of the diamond-bearing kimberlite pipes recently discovered there. Coinciding with increased industrial development, the prevalence of hunting camps in the region is increasing. Some outfitters in the study area are becoming increasingly vocal about raising the current quota for the sport harvest of grizzly bears.

We believe any increase in current harvest quotas would have a considerable impact on the population. Mortality of females (and especially females with cubs) from all sources of harvest must be minimized. Removal rates used in our risk assessments are based on past patterns of harvest; thus, selectivity and vulnerability rates used in our analyses assume that bears removed from the population will be primarily subadults or adult males. If females with cubs contribute more to the reported harvest than in the past (i.e., as problem kills at mine sites or camps), risks of population decline will increase.

To refine our models we would need to decrease uncertainty in input parameters, especially subadult survival, for which rate of increase is quite sensitive (Hovey and McLellan, 1996), and initial population size. Our modeling results were sensitive to the SE applied to initial population size. Both subadult survival and population size, however, are difficult and costly to estimate. Estimating subadult survival would require a tracking study of two- and three-year-old bears captured prior to dispersal from their mother. Subadult bears in the central Arctic travel over extremely large distances ( $> 20\,000$  km<sup>2</sup>; McLoughlin, 2000) and would need to be tracked using expensive satellite radio-collars. Most two- and three-year-old bears,

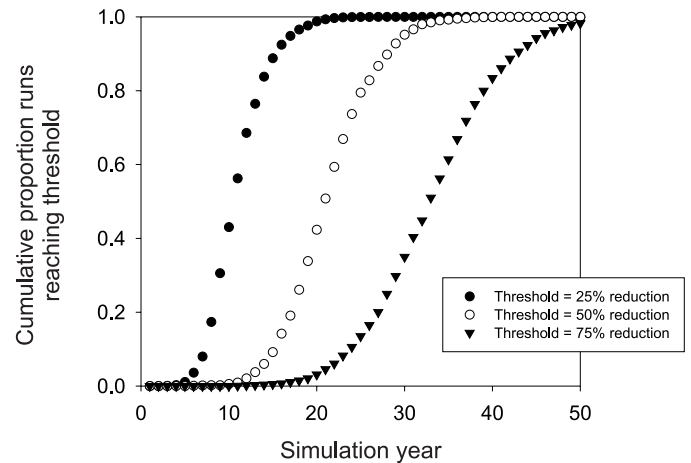


FIG. 6. RISKMAN projection simulations performed with the same mean harvest rate of 13.4 bears per year as in Figure 3, but including as unconfirmed mortalities 7 missing bears for which no collar was recovered.

however, are probably too small and grow too rapidly to be collared safely.

Estimating population size would be even more costly, and would likely involve a lengthy mark-recapture program. Although expensive, an estimate of population size using mark-recapture methods would provide not only an objective and more precise estimate of the number of bears in the central Arctic, but also the means for obtaining new estimates for rates of survival and population increase (i.e., by using the Cormack-Jolly-Seber method; Krebs, 1989). Comparing rates of increase with those contained in this study and McLoughlin and Messier (2001) would provide an excellent opportunity to identify the direction of growth for the population. For this reason, perhaps it would be wise to delay estimating population size using mark-recapture methods for some time in the future (e.g., 5–10 years). This would permit enough time to lapse between studies to better gauge the effects of current management practices on maintaining the population's rate of increase.

#### ACKNOWLEDGEMENTS

Numerous private-sector and government sponsors have contributed to the grizzly bear project, including the West Kitikmeot/Slave Study Society, BHP Diamonds Inc., BHP Minerals, Diavik Diamond Mines Inc., the Government of the Northwest Territories, the University of Saskatchewan, RESCAN Environmental Services Ltd., Axys Environmental Consulting Ltd., the Nunavut Wildlife Management Board, the Federal Department of Indian Affairs and Northern Development, the Polar Continental Shelf Project, the Northwest Territories Centre for Remote Sensing, Echo Bay Mines Ltd., Air Tindi Ltd., First Air Ltd., Big River Air Ltd., Canadian Helicopters Ltd., Nunasi Helicopters, Helicopter Wildlife Management Ltd., the Northern Scientific Training Program, and the Natural Sciences and Engineering Research Council of Canada.

## REFERENCES

- BOYCE, M.S. 1992. Population viability analysis. *Annual Review in Ecology and Systematics* 23:481–506.
- . 1995. Population viability for grizzly bears (*Ursus arctos horribilis*): A critical review. Report to the Interagency Grizzly Bear Committee. Washington, D.C.: U.S. Fish and Wildlife Service.
- CASE, R.L., and BUCKLAND, L. 1998. Reproductive characteristics of grizzly bears in the Kugluktuk area, Northwest Territories, Canada. *Ursus* 10:41–47.
- CAUGHLEY, G. 1977. Analysis of vertebrate populations. New York: John Wiley & Sons.
- COSEWIC (COMMITTEE ON THE STATUS OF ENDANGERED WILDLIFE IN CANADA). 2000. List of species at risk. Ottawa: Canadian Wildlife Service.
- EASTRIDGE, R., and CLARK, J.D. 2001. Evaluation of 2 soft-release techniques to reintroduce black bears. *Wildlife Society Bulletin* 29:1163–1174.
- EWENS, W.J., BROCKWELL, P.J., GANI, J.M., and RESNICK, S.I. 1987. Minimum viable population sizes in the presence of catastrophes. In: Soulé, M., ed. *Viable populations for conservation*. New York: Cambridge University Press. 59–68.
- FERGUSON, S.H., and McLOUGHLIN, P.D. 2000. Effect of energy availability, seasonality, and geographic range on brown bear life history. *Ecography* 23:193–200.
- GAU, R.J. 1998. Food habits, body condition, and habitat of the barren-ground grizzly bear. M.Sc. Thesis, University of Saskatchewan, Saskatoon.
- HOVEY, F.W., and McLELLAN, B.N. 1996. Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates. *Canadian Journal of Zoology* 74:1409–1416.
- KREBS, C. 1989. *Ecological methodology*. New York: Harper Collins.
- LACY, R.C. 1993. VORTEX: A computer simulation model for population viability analysis. *Wildlife Research* 20:45–65.
- LESLIE, P.H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33:183–212.
- LINDENMAYER, D.B., BURGMAN, M.A., AKÇAKAYA, H.R., LACY, R.C., and POSSINGHAM, H.P. 1995. A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modeling the viability of wildlife populations. *Ecological Modelling* 82:161–174.
- McLELLAN, B.N. 1994. Density-dependent population regulation of brown bears. In: Taylor, M., ed. *Density-dependent population regulation in black, brown, and polar bears*. Proceedings of the International Conference on Bear Research and Management. Monograph Series No. 3:15–24.
- McLOUGHLIN, P.D. 2000. The spatial organization and habitat selection patterns of barren-ground grizzly bears in the central Arctic. Doctoral dissertation, University of Saskatchewan, Saskatoon.
- McLOUGHLIN, P.D., and MESSIER, F. 2001. The demography of barren-ground grizzly bears (*Ursus arctos*) in Nunavut and the Northwest Territories. Unpubl. ms. Available from the Department of Resources, Wildlife, and Economic Development, Government of the Northwest Territories, #600, 5102 – 50 Avenue, Yellowknife, NT X1A 3S8, Canada. URL <http://www.nwtwildlife.rwed.gov.nt.ca/publications/otherreports.htm>.
- McLOUGHLIN, P.D., CASE, R.L., GAU, R.J., FERGUSON, S.H., and MESSIER, F. 1999. Annual and seasonal movement patterns of barren-ground grizzly bears in the central Northwest Territories. *Ursus* 11:79–86.
- McLOUGHLIN, P.D., FERGUSON, S.H., and MESSIER, F. 2000. Intraspecific variation in home range overlap with habitat quality: A comparison among brown bear populations. *Evolutionary Ecology* 14:39–60.
- McLOUGHLIN, P.D., CLUFF, H.D., and MESSIER, F. 2002. Denning ecology of barren-ground grizzly bears in the central Arctic. *Journal of Mammalogy* 83:188–198.
- MILLS, L.S., HAYES, S.G., BALDWIN, C., WISDOM, M.J., CITTA, J., MATTSON, D.J., and MURPHY, K. 1996. Factors leading to different viability predictions for a grizzly bear data set. *Conservation Biology* 10:863–873.
- TAYLOR, M., and CARLEY, J.S. 1988. Life table analysis of age structured populations in seasonal environments. *Journal of Wildlife Management* 52:366–373.
- TAYLOR, M.K., CARLEY, J.S., and BUNNELL, F.L. 1987. Correct and incorrect use of recruitment rates for marine mammals. *Marine Mammal Science* 3:171–178.
- TAYLOR, M.K., KUK, M., OBBARD, M., CLUFF, H.D., and POND, B. 2001. RISKMAN: Risk analysis for harvested populations of age-structured, birth-pulse species. Software Manual. Unpubl. ms. Available at P.O. Box 1000, Department of Sustainable Development, Government of Nunavut, Iqaluit, NU X0A 0H0, Canada.
- TRENT, T.T., and RONGSTAD, O.J. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. *Journal of Wildlife Management* 38:459–472.
- WHITE, G.C. 2000. Population viability analysis: Data requirements and essential analyses. In: Boitani, L., and Fullers, T.K., eds. *Research techniques in animal ecology: Controversies and consequences*. New York: Columbia University Press. 288–331.
- WIELGUS, R.B. 2002. Minimum viable population and reserve sizes for naturally regulated grizzly bears in British Columbia. *Biological Conservation* 106:381–388.