

Martine Landry
Vernon G. Thomas
Thomas D. Nudds

Sizes of Canadian National Parks and the Viability of Large Mammal Populations: Policy Implications

Introduction

Canada's 39 national parks are intended to form a system of representative natural regions across the country. These parks are dedicated to the public for their benefit and education, while being maintained in an unimpaired state for future generations (Parks Canada 2000). However, the size and boundaries of the parks reflect competition from logging, mining, agriculture, and urban development occurring around them (Parks Canada 2000). There is renewed public and governmental concern about maintaining and restoring the ecological integrity of Canadian national parks. Most northern parks are still surrounded by wilderness, but southern parks are challenged from within and without by stresses that reduce ecosystem viability (Parks Canada 2000). Parks Canada has identified significant threats to all but one of the parks (Canadian Heritage 1998). The current zoning system for national parks is more reflective of historical land uses and facilities rather than designating lands within parks according to criteria for ecological integrity, and especially the temporal and spatial dynamics of wildlife populations (Parks Canada 2000).

Recent research (Newmark 1987, 1995; Glenn and Nudds 1989; Grumbine 1990; Gurd and Nudds 1999; Nudds et al. 1998a; Parks Canada 2000) has shown that North American parks do not protect many of the wild species that depend on them. Parks Canada is aware that managing parks as isolated areas is no longer appropriate, and that the parks' resources and value to visitors are

being compromised by external land-use factors under provincial control as well as internal factors related to public use (Green 1984). Under the existing park zoning system, there is provision for legal protection of wilderness areas to prevent activities that could impair the ecological integrity of the parks (Canadian Heritage 1999; Parks Canada 2000). However, estimates of the minimum necessary size of parks

vary considerably (Gurd et al. in press), leading to different policy implications for management.

Most parks may not include large areas of pristine wilderness for their flora and fauna, and the status of such species may depend upon what happens outside of park boundaries. We examined whether Canadian national parks, as isolated areas, could sustain indefinitely their populations of wolves (*Canis lupus*), black bears (*Ursus americanus*), and grizzly bears (*Ursus horribilis*). These species were selected because the minimum area requirement for mammals is usually larger than for other taxa, and because they are most sensitive to isolation and reduced habitat area (Schmiegelow and Nudds 1987). Mammalian carnivores also have larger home ranges than omnivores or herbivores of similar body size (Harestad and Bunnell 1979).

If the populations of these carnivores are deemed to be viable within the actual wilderness areas of the national parks, there is potential for these species to be managed sustainably within the parks. However, if the minimum critical area (MCA; Nudds et al. 1998b: 356) required for these three species exceeds the total useable area of habitat inside the parks, then provision to create legally protected areas of wilderness elsewhere must be made.

Methods

The MCA for each species was calculated from the equation $MCA = MVP/MVPD$, where MVP is the minimum viable population size and

MVPD is the minimum viable population size density. The MVP is that population size large enough to allow long-term persistence despite unpredictable genetic, demographic, and environmental changes (Shaffer 1981; Fritts and Carbyn 1995). The MVP can be affected by these parameters: sex ratio, age at first breeding (L), litter size, survival rate to age of first breeding (l), probability of breeding (b), and age distribution in the population (Table 1). The model of Reed et al. (1986) used to calculate the MVP is based on these parameters. This model applies to species with overlapping generations, and may be adjusted for monogamous species, such as wolves, or polygamous species, such as black bears and grizzly bears.

An effective population size of 500 individuals was used for both the monogamous and polygamous species. This effective population size is that which has been hypothesized to be sufficient to avoid the loss of genetic variability due to inbreeding and to minimize the effects of genetic drift over a long period of time (Reed et al. 1986). Estimates for demographic parameters used to calculate the MVP were derived from published studies (Table 1). A sex ratio of 1M:1F for adults was assumed for all species, even though such a ratio could be confirmed from the literature for only cubs and yearlings. Because direct information on the breeding sex ratio was lacking for black bears and grizzly bears, different MVP sizes (and an average MVP size) for these species were calculated using different sex ratios (Table 1).

Table 1. Different MVPs with derived MCAs for wolves, grizzly bears, and black bears using the model developed by Reed et al. (1986) with different parameters.

Species	Parameters	MVP	MCA (sq km)
Wolves ¹	Largest L ; sex*, breeding 1:1	530	768 ⁴
	Smallest L ; sex 1:1, breeding 1:3	1,178	1,707 ⁵
Grizzly bears ²	Largest L, l, b; sex, breeding 1:1	388	1,911 ⁴
	Largest L, l, b; sex 1:1, breeding 1:3	488	2,404
	Largest L, smallest l, b; sex, breeding 1:1	1,198	5,901
	Largest L, smallest l, b; sex 1:1, breeding 1:3	1,108	5,458
	Smallest L, l, b; sex, breeding 1:1	2,222	10,946 ⁵
	Smallest L, l, b; sex 1:1, breeding 1:3	1,900	9,360
	Smallest L, largest l, b; sex, breeding 1:1	710	3,498
	Smallest L, largest l, b; sex 1:1, breeding 1:3	776	3,823
	Averages; sex, breeding 1:1	656	3,429
Black bears ³	Largest L, l, b; sex, breeding 1:1	462	1,717 ⁴
	Smallest L, l, b; sex, breeding 1:1	4,296	15,970 ⁵
	Averages; sex, breeding 1:1	982	3,651
	Averages; sex 1:1, breeding 1:3	1,336	4,967

* Sex ratio and breeding ratio 1:1

1. Carbyn (1988), Soper (1973), Hart and Grossenheider (1978), Gensler and Quintin (1983), Carbyn et al. (1993), Haber (1977), Blech (1977).

2. van Tighem (1987), Hart and Grossenheider (1978), Soper (1973), Reynolds (1983), Pearson (1976), Mandry and Flout (1973), Wiegler et al. (1984), Knight and Eschwert (1985), Mitchell (1988a, 1988b).

3. van Tighem (1987), Gensler and Quintin (1983), Hart and Grossenheider (1978), Soper (1973), Yodanis and Kolomojty (1988), Schwartz and Forman (1981), Keay (1985), Neubauer et al. (1988), Elmer and Wensel (1988).

4. Best-case (optimistic) scenario.

5. Worst-case (pessimistic) scenario.

Best- and worst-case scenarios were calculated for each species. The best-case scenario determined the smallest viable population size, whereas the

worst-case scenario determined the largest viable population size. This was accomplished by using different values for different parameters and breeding

ratios of 1M:1F or 1M:3F (Table 1). Once the best- and worst-case scenarios had been determined for grizzly bears, the same array of values was used for black bears. Cubs, yearlings, adult non-breeders, and adult failed-breeders were excluded from the calculations; therefore, estimates of MVP size are very conservative, referring only to the numbers of breeding animals.

The MVPD of each species was estimated from the species' body mass (Silva and Downing 1994). Published values of the body mass of adult males and females of each of the three species from different regions of North America were combined into a single body mass estimate for each species. Finally, the best-case and other derived MCAs for each species were compared with the sizes of those national parks where the species is, or was historically, present (Banfield 1974).

Results

The sizes of most Canadian national parks are similar to the sum of their designated preservation and wilderness areas (i.e., Zones 1 and 2 in the Parks Canada terminology; Table 2). Therefore, we compared the total area of parks with the calculated MCAs. The estimated minimum viable population densities were 0.69 wolves/sq km, 0.27 black bears/sq km, and 0.20 grizzly bears/sq km. The smallest MCA calculated for the three species was 768 sq km for wolves; the largest, 15,970 sq km for black bears (Table 1).

Eighteen of Canada's 39 parks are

less than 1,000 sq km in area, and 14 of those 18 are smaller than 500 sq km (Figure 1). Of the 36 national parks that either presently contain or historically contained at least one of the three species under study, 14 appear unlikely to be able to sustain any of the three species, under even the best-case scenario (Figure 1a). Only 6 of the 36 parks are larger than 15,970 sq km and thus might be able to sustain all three species under the worst-case scenario. In the best-case scenario for grizzly bears, 42% of the national parks that either presently contain or historically contained this species are too small to sustain the MVP, and only 17% could sustain the worst-case MVP (Figure 1b). Similar results pertain to black bears: 63% of the parks are too small to sustain a population under the best-case scenario, and only 7% could do so under the worst-case scenario (Figure 1c).

Figure 1 also reveals differences in the MCAs among species. The MCA for wolves is less than that for both black bears and grizzly bears, as is to be expected from the wolf's smaller body mass. However, the worst-case scenario for black bears predicts the need for a greater area of habitat than that predicted by the worst-case scenario for grizzly bears, a result inconsistent with what would be expected from a comparison of the body mass of these two species.

Discussion

On an individual basis, national parks are representative of the larger Canadian ecozones in which they are

Table 2. Total area for Canadian national parks and their special preservation areas (Zone 1) and wilderness areas (Zone 2), in the park zoning system, Zone 1 does not permit public access, and Zone 2 allows activities with minimal human interference (Canadian Heritage 1996).

National Park / Species	Total Area	Zone 1	Zone 2
		(area in sq km)	
Saint Lawrence Islands	8.7	3	2
Point Pelee (w, bb)	15	11	0
Prince Edward Island	21.5	5	0
Georgian Bay Islands (w, bb)	25.6	4	0
Mingan Archipelago (w, bb)	151	15	134
Bruce Peninsula (w, bb)	154	75	0
Elk Island (w, bb)	194	0	177
Fundy (w, bb)	206	2	183
Kouchibouguac (w, bb)	239	10	129
Forillon (w, bb)	240	3	231
Mount Revelstoke (w, gb, bb)	256	97	62
Terra Nova (w, bb)	400	4	296
Kejimikujik (w, bb)	404	16	311
Pacific Rim (w, bb)	500	6	295
Waterton Lakes (w, gb, bb)	505	10	399
La Mauricie (w, bb)	536	11	498
Grasslands (w, bb)	906	18	0
Cape Breton Highlands (w, bb)	948	142	683
Yoho (w, gb, bb)	1,313	26	1,116
Glacier (w, gb, bb)	1,349	0	1,093
Kootenay (w, gb, bb)	1,406	84	1,294
Gwaii Haanas	1,495	75	1,420
Gros Morne (w, bb)	1,805	126	1,101
Pukaskwa (w, bb)	1,878	3	1,863
Riding Mountain (w, bb)	2,973	15	2,914
Prince Albert (w, bb)	3,874	4	3,853
Nahanni (w, gb, bb)	4,765	14	4,741
Banff (w, gb, bb)	6,641	266	6,176
Jasper (w, gb, bb)	10,878	54	10,660
Auyuittuq (w)	19,469	215	21,254
Kluane (w, gb, bb)	22,013	132	21,793
Quttinirpaaq (w)	37,775	189	37,397
Wood Buffalo (w, bb)	44,802	4,480	38,530
Tuktut Nogait (w, gb)	16,340	—	—
Sirmilik (w)	22,252	—	—
Wapusk (w, bb)	11,475	—	—
Aulavik (w)	12,200	—	—
Ivvavik (w, gb)	9,750	—	—
Vuntut (w, gb, bb)	4,345	—	—

Species currently or historically present: w - wolf, bb - black bear, gb - grizzly bear.

Source: Don H. Howard, Parks Canada, Natural Resources Branch, Parks Canada, Hull, Quebec (personal communication, February 2000).

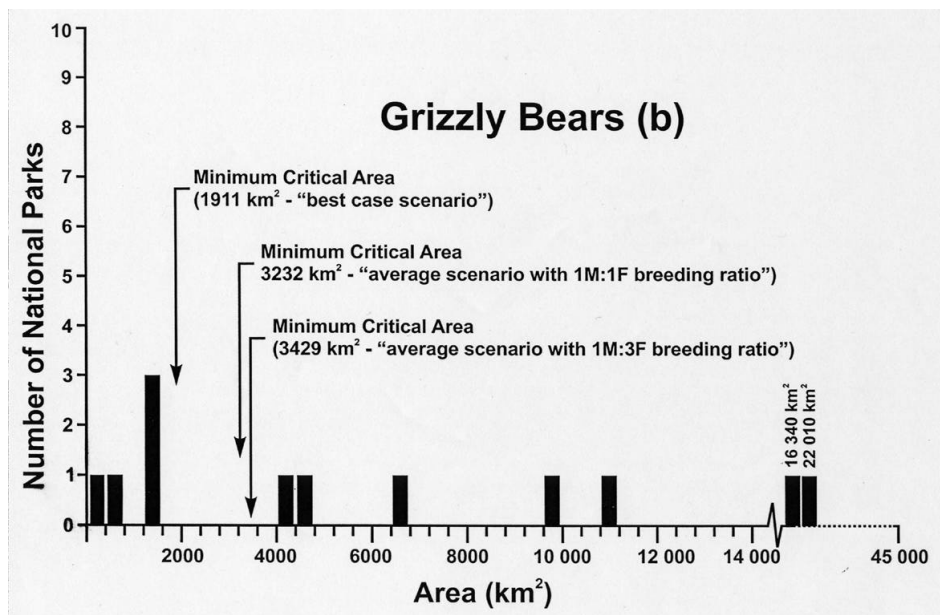
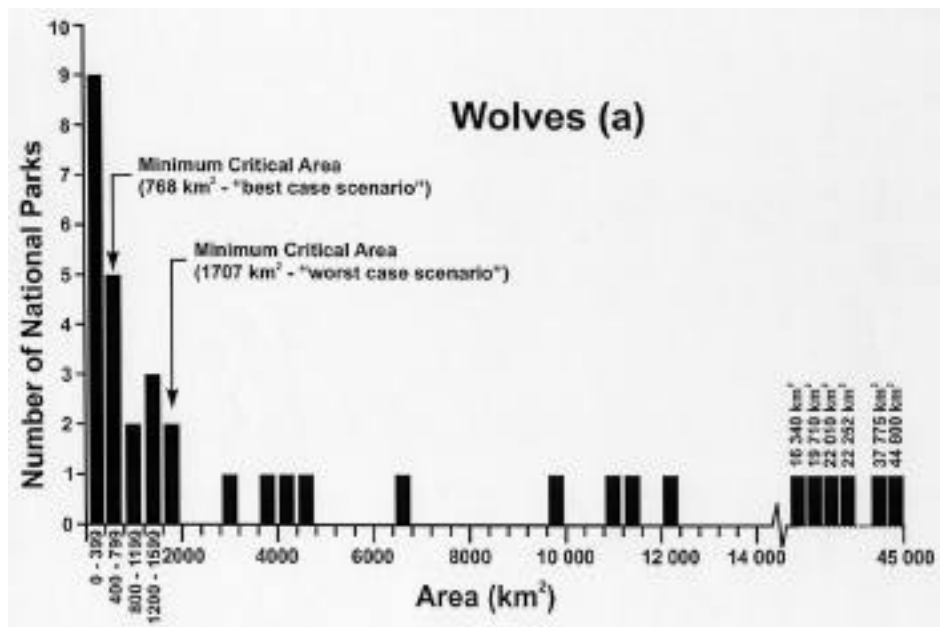
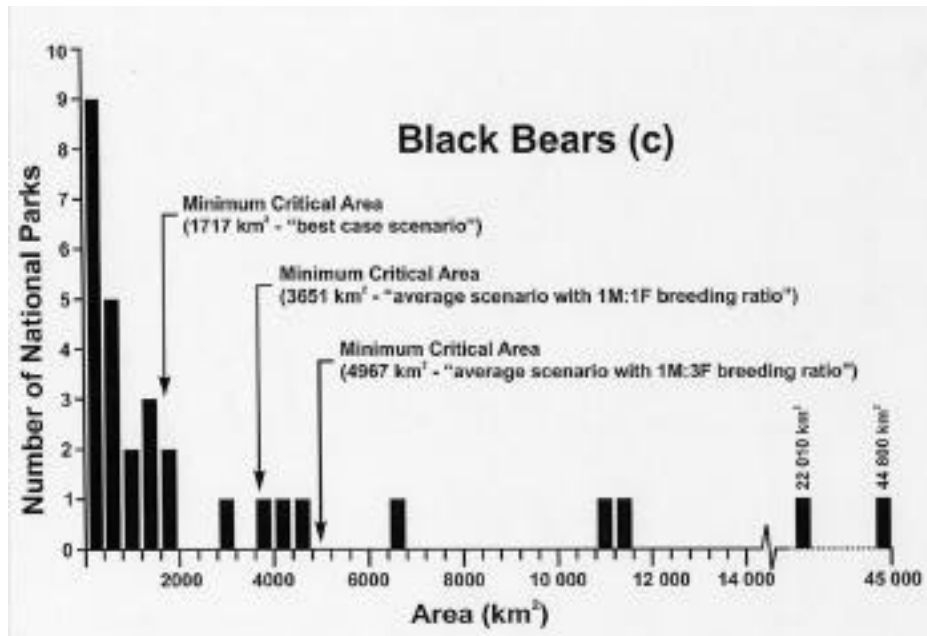


Figure 1. The number of national parks that are smaller or greater than the ranges of minimum critical areas of wolves (a), grizzly bears (b), and black bears (c). Only Canadian national parks in which the species under study were currently or historically present are included.

Figure 1 (cont'd)



located (Parks Canada 1999). Only the most northerly parks are still surrounded by wilderness, are not yet subject to over-use, and have few land-use conflicts outside their boundaries. The small size, high visitation rates, and ecological isolation of southern parks militate against MVPs of wolves, black bears, and grizzly bears being maintained there. Even within protected areas, conflicts with humans are usually the major cause of adult mortality in these species (Woodroffe and Ginsberg 1998).

This study shows that most of Canada's national parks cannot indefinitely sustain MVPs of these large carnivorous mammals. The number of parks whose areas are smaller than the required MCA increases from 14 of the

36 parks in the best-case scenario to 30 of the 36 parks in the worst-case scenario. Therefore, priority should be given to those preservation measures that maximize reserve size or mitigate carnivore persecution along park borders and in buffer zones (Woodroffe and Ginsberg 1998). Parks Canada has recently, and correctly, moved to designate wilderness protection through zoning in national parks. However, because most parks are already too small to adequately protect large mammals, it follows that existing wilderness zones within parks will be too small, regardless of the zoning schemes used.

There are sources of error in the determination of the MCA for each of these species. The total areas of the

parks include unusable habitat features such as lakes, steep mountain faces, glaciers, and human developments. There are several major assumptions of the Reed et al. (1986) model that can be violated in real, wild, populations. We included only adult male and adult females in the determination of each species' MVP. It is not realistic to have only breeders in the defined population, especially for wolves that live in a highly-structured social pack system (Mech 1966). Violation of any of the assumptions results in underestimation of the number of breeders required to maintain the effective population size of 500 individuals. The conventional use of 500 as an effective population size has also been questioned. An overview analysis such as this cannot account for environmental stochasticity or variations in the local richness of habitats. Together, these sources of error may explain discrepancies between the calculated MCAs and observed populations that survive in small areas or which are extirpated from larger areas, or the discrepancy between the MCAs for two bear species in this study.

Because most national parks are smaller than the MCAs required by their large carnivores, Parks Canada should work to ensure that wilderness areas both outside and inside the parks are preserved. In many cases, large mammals are currently in national parks only because there is wilderness surrounding the park boundaries. The ability of large carnivore populations to use wild habitats adjacent to parks and

their probability of survival within the parks are highly correlated (Newmark 1995). This situation is evident in the case of black bears inhabiting Atlantic Canada's national parks. The normal movements of foraging black bears are so extensive that they and their habitats should be managed on a landscape scale exceeding park boundaries (Forbes et al. 1999). Reducing the losses of large mammals in the future will require that the total area of species habitats in parks be augmented either through the acquisition or the cooperative management of non-federal lands adjacent to parks (Newmark 1987).

The size and location of many protected areas have been based on convenience or compromise with competing land uses (Nudds et al. 1998b). Most boundaries are artificial and do not reflect the biotic boundaries of the local ecosystem. The results of this study allow us to concur with the recommendations of the Panel on the Ecological Integrity of Canada's National Parks (Parks Canada 2000) that urge a review of the park zoning system and consideration of parks as multi-scaled ecosystems. Functional habitat connections between parks and adjacent protected areas should be created, maintained, or restored to allow movements of wild species (Parks Canada 2000). This would permit populations to be managed at sizes that might more likely persist.

Attempts are already occurring to introduce park perimeter protection under Parks Canada directive, as in the case of Georgian Bay Islands National

Park and the Greater Georgian Bay Ecosystem Initiative (Wiersma 1996), the Foothills Model Forest near Jasper National Park (Parks Canada 2000), and the Greater Fundy Ecosystem project (Woodley and Freedman 1995). These initiatives are positive steps toward a more multi-level-oriented collaboration among different agencies. However, the criteria for zoning within parks need to be reviewed. Zoning categories are weakly defined in terms of the preservation of ecological values (Parks Canada 2000). New zoning criteria, if they are to benefit wildlife, should reflect the range and habitat requirements of species of concern and be based on their ecological needs, rather than on the placement of proposed developments and user facilities.

The provinces, territories, and private land owners will play a key role in the future of Canadian national parks, especially in southern Canada, where agreements to decrease outside land-use stresses might contribute to preserving large-animal populations. In the creation of new parks, Parks Canada and the provinces should use their legal powers to protect against development adjacent to boundaries. These, too, would serve to effectively enhance the size of parks and promote the persistence of large-animal populations. Management arrangements with neighboring jurisdictions can have a profound effect upon the sustainability of large species and the ecological integrity of parks (Parks Canada 2000).

Acknowledgments

We would like to thank Don H. Rivard of Parks Canada for providing information on areas and zoning of national parks. We thank Ian Smith, University of Guelph Department of Zoology, for preparing the figures and tables, and Yolanda Wiersma for helpful comments on an earlier draft.

References

- Banfield, A.W.F. 1974. *The Mammals of Canada*. Toronto: University of Toronto Press.
- Beaudin, L., and M. Quintin. 1983. *Guide des mammifères terrestres*. Québec, Québec: Éditions Michel Quintin.
- Burt, W.H., and R.P. Grossenheider. 1976. *A Field Guide to the Mammals of North America*. Peterson Field Guide Series. Boston: Houghton Mifflin.
- Canadian Heritage, Parks Canada. 1998. *State of the Parks 1997 Report*. Ottawa: Minister of Public Works and Government Services Canada. <<http://www.parkscanada.pch.gc.ca/library/>>.
- . 1999. *Land Use Zoning Protection in Canada's National Parks*. <http://parkscanada.pch.gc.ca/natress/inf_pal/eco_des/zoning/lan_usee.htm>.
- Carbyn, L.N. 1981. *Wolves in Canada and Alaska*. Canadian Wildlife Service Report Series No. 45. Ottawa: Canadian Wildlife Service.
- Carbyn, L.N., S. M. Oosenbrug, and D.W. Anions. 1993. *Wolves, Bison ... and the Dynamics Related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park*. Edmonton Alta.: Canadian Circumpolar Institute, University of Alberta.
- Elowe, K.D., and W.E. Wendell. 1989. Factors affecting black bear reproductive success and cub survival. *Journal of Wildlife Management* 53:4, 962-968.

- Forbes, G., E. Daigle, and Parks Canada Atlantic Region. 1999. *Black Bear Ecology and Management Issues for Atlantic Canadian National Parks*. Parks Canada Ecosystem Science Review Reports No. 13. Halifax, N.S.: Parks Canada.
- Fritts, S.H., and L.N. Carbyn. 1995. Population viability, nature reserves, and the outlook for gray wolf conservation in North America. *Restoration Ecology* 3:1, 26-38.
- Glenn, S.M., and T.D. Nudds. 1989. Insular biogeography of mammals in Canadian parks. *Journal of Biogeography* 16, 261-268.
- Green, T. 1984. *Workshop on Future Parks Canada Strategies 1986-2001*. Waterloo, Ont.: Heritage Resources Program, University of Waterloo, and Parks Canada.
- Grumbine, R.E. 1990. Viable populations, reserve size, and federal lands management: A critique. *Conservation Biology* 4:2, 127-134.
- Gurd, D.B., and T.D. Nudds. 1999. Insular biogeography of mammals in Canadian parks: A re-analysis. *Journal of Biogeography* 26, 973-982.
- Gurd, D.B., T.D. Nudds, and D.H. Rivard. In press. Conservation of mammals in eastern North American wildlife reserves: How small is too small? *Conservation Biology*.
- Haber, G.C. 1977. *Socio-ecological Dynamics of Wolves and Prey in a Subarctic Ecosystem. Volume 2*. Ann Arbor, Mich.: University Microfilms International.
- Harestad, A.S., and F.L. Bunnell. 1979. Home range and body weight—A reevaluation. *Ecology* 60:2, 389-402.
- Kasbohm, J.W., M.R. Vaughan, and J.G. Kraus. 1996. Effects of gypsy moth infestation on black bear reproduction and survival. *Journal of Wildlife Management* 60:2, 408-416.
- Keay, J.A. 1995. Black bear reproductive rates in Yosemite National Park. *California Fish and Game* 81:3, 122-131.
- Knight, R.R., and L.L. Eberhardt. 1985. Population dynamics of Yellowstone grizzly bears. *Ecology* 66:2, 323-334.
- McLellan, B.N. 1989a. Dynamics of a grizzly bear population during a period of industrial resource extraction, I: Density and age-sex composition. *Canadian Journal of Zoology* 67, 1856-1860.
- . 1989b. Dynamics of a grizzly bear population during a period of industrial resource extraction, II: Mortality rates and causes of death. *Canadian Journal of Zoology* 67, 1861-1864.
- Mech, L.D. 1966. *The Wolves of Isle Royale*. Fauna of the National Parks of the United States No. 7. Washington, D.C. National Park Service.
- . 1977. Productivity, mortality, and population trends of wolves in northeastern Minnesota. *Journal of Mammalogy* 58:4, 559-574.
- Mundy, K.R.D., and D.R. Flook. 1973. *Background for Managing Grizzly Bears in the National Parks of Canada*. Canadian Wildlife Service Report Series No. 22. Ottawa: Canadian Wildlife Service.
- Newmark, W.D. 1987. A land-bridge island perspective on mammalian extinctions in western North American parks. *Nature* 325, 430-432.
- . 1995. Extinction of mammal populations in western North American national parks. *Conservation Biology* 9:3, 512-526.
- Nudds, T.D., D.B. Gurd, C.P. Henschel, and C.G. McLaughlin. 1998a. Use of estimated “pristine” species-area relations as null models for evaluating size and integrity standards for protected areas: An update. Pp. 143-152 in *Parks and Protected Areas Research in Ontario 1998*. J.G. Nelson, K. Van Osch, T. J. Beechey, W.R. Stephenson, and J. Marsh, eds. Waterloo, Ont.: Parks Research Forum of Ontario, Heritage Resources Centre, University of Waterloo.
- Nudds, T.D., C.P. Henschel, J.K. Kerr, D. Currie, L. Fahrig, S. Koh, and C.G. McLaughlin. 1998b. Protected area networks: Assessment of Ontario’s “Nature’s Best” action plan and recommendations. Pp. 363-372 in *Parks and Protected Areas Research in Ontario 1998*. J.G. Nelson, K. Van Osch, T. J. Beechey, W.R. Stephenson, and J. Marsh, eds. Waterloo, Ont.: Parks Research Forum of Ontario, Heritage Resources Centre, University of Waterloo.
- Parks Canada. 1999. *Terrestrial Ecozones of Canada*. <http://parksCanada.pch.gc.ca/natress/inf_pa1/ECO_DES/ECOZONES/ZONE_00E.htm>.
- . 2000. *“Unimpaired for Future Generations”? Conserving Ecological Integrity with Canada’s National Parks*. 2 vols. Report of the Panel on the Ecological Integrity of Canada’s National Parks. Ottawa: Minister of Government Works and Public Services Canada.

- Pearson, A.M. 1975. *The Northern Interior Grizzly Bear Ursus arctos L.* Canadian Wildlife Service Report Series No. 34. Ottawa: Canadian Wildlife Service.
- Reed, J.M., P.D. Doerr, J.R. Walters. 1986. Determining minimum population sizes for birds and mammals. *Wildlife Society Bulletin* 14, 255-261.
- Reynolds, H. 1993. *Evaluation of the Effects of Harvest on Grizzly Bear Population Dynamics in the Northcentral Alaska Range.* Juneau: Alaska Department of Fish and Game.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31, 131-134.
- Schmiegelow, F.K.A., and T.D. Nudds. 1987. Island biogeography of vertebrates in Georgian Bay Islands National Park. *Canadian Journal of Zoology* 65, 3041-3043.
- Schwartz, C.C., and A.W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. *Wildlife Monographs* 113, 1-58.
- Silva, M., and J.A. Downing. 1994. Allometric scaling of minimal mammal densities. *Conservation Biology* 8:3, 732-743.
- Soper, J.D. 1973. *The Mammals of Waterton Lakes National Park, Alberta.* Canadian Wildlife Service Report Series No. 23. Ottawa: Canadian Wildlife Service.
- van Tighem, K. 1997. *Bears: An Altitude Superguide, the Canadian Rockies.* Vancouver, B.C.: Altitude Superguides.
- Wielgus, R.B., F.L. Bunnell, W.L. Wakkinen, and P.E. Zager. 1994. Population dynamics of Selkirk Mountain grizzly bears. *Journal of Wildlife Management* 58:2, 266-272.
- Wiersma, Y. 1996. Corridors in a regional conservation plan: A commentary on the use of corridors using the Greater Georgian Bay Ecosystem as a model. *The George Wright Forum* 13:4, 51-62.
- Woodley, S., and B. Freeman. 1995. The Greater Fundy Ecosystem Project: Towards ecosystem management. *The George Wright Forum* 12:1, 7-15.
- Woodroffe, R., and J.R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280, 2126-2128.
- Yodzis, P., and G.B. Kolenosky. 1986. A population dynamics model of black bears in eastcentral Ontario. *Journal of Wildlife Management* 50:4, 602-612.

Martine Landry, Vernon G. Thomas, and Thomas D. Nudds, Department of Zoology, College of Biological Science, University of Guelph, Guelph, Ontario N1G 2W1, Canada; vthomas@uoguelph.ca

