11. The methods used in this study are fundamentally similar to those previously summarized in detail (6, 7). Briefly, food-deprived adult male Long-Evans rats (Harlan) were trained to chase randomly dropped food pellets (Bio-Serv) in a 51-cm-high gray cylinder (76-cm diameter) with a white card mounted on one wall to provide an asymmetrical cue. After being thoroughly familiarized with the task and environment, animals were implanted stereotactically (anterior, −2 mm; lateral, 1.8 mm; dorsal, 2 mm) with a drivable 10-wire (25-μm nichrome) microelectrode array about 1 mm dorsal to the CA1 hippocampal pyramidal cell layer. At least 5 days after surgery, animals were screened for units while chasing pellets in the gray cylinder. Units were amplified 10,000 times and bandpass filtered at 300 to 10,000 Hz. The amplifier output was digitized at 40 kHz. When at least two place cells could be simultaneously recorded in the gray cylinder, cue control was tested by rotating the cylinder 90°. In all cases, all fields rotated 90° (28). The next day, after one 8-min test session (D1G0) in the gray cylinder (the familiar environment), animals were injected intraperitoneally (ip) with either saline or CPP (10 mg/kg) and returned to their cages for an hour. All other recording sessions were 16 min. The intervals between sessions are shown in the legend for Fig. 1. Animals were always returned to their home cage between recording sessions. Units were analyzed offline with the Discovery CP Analysis and Autocut software packages (Datawave, Longmont, CO). Although it is possible that in some cases a "unit" was really two neurons, this would have worked against our main findings by increasing the variability of the data.

12. The rate maps produced by a given cell in two sessions were treated as two lists of numbers for the calculation of a correlation coefficient. The values of correlation coefficients for all cells from an animal were averaged to provide a mean "similarity" score. Cells that had an overall firing rate of less than 0.1 spikes per second in both sessions were excluded from quantitative analysis.

13. Peak firing rate is the rate in the three by three block of pixels with the highest average rate. Coherence is the z transform of the correlation coefficient between the rate of a pixel and the average rate of its eight nearest neighbors. Signal-to-noise ratio is the number of in-field spikes divided by the total number of spikes in a session. Information content = $\Sigma P_i (R_i/R) \log_2 (R_i/R)$, where i is the bin number, P_i is the probability for occupancy of bin i, R_i is the mean firing rate for bin i, and R is the overall mean firing rate {from E. Markus et al. [Hippocampus 4, 410 (1994)]}. Running speed was calculated every 0.25 s and averaged across the session.

14. For saline-injected rats, the similarity of D1G1 to D1W1 was −0.006 ± 0.014, and the similarity of D1G1 to D2G2 was 0.565 ± 0.037 [t (10) = 6.55, P = 6.5 × 10⁻⁵ comparing the two similarity scores]. For CPP-injected rats, the similarity of D1G1 to D1W1 was 0.170 ± 0.044, and the similarity of D1G1 to D2G2 was 0.466 ± 0.065 [t (10) = 3.32, P = 7.8 × 10⁻³].

15. L. Ward et al., Pharmacol. Biochem. Behav. 35, 785 (1990).

16. H. V. Curran, Biol. Psychol. 23, 179 (1986); T. U. Jarbe, Acta Neurol. Scand. Suppl. 109, 37 (1986).

17. D. M. Diamond et al., J. Neurosci. 8, 4079 (1988); J. Larson and G. Lynch, Brain Res. 441, 111 (1988).

18. Male Long-Evans rats (Charles River Laboratories) were anesthetized and implanted with two twisted pairs of Teflon-coated stainless steel wires (127-μm diameter) for stimulation and recording. The recording electrode was positioned in the pyramidal layer of the CA1 region of the hippocampus, and the stimulating electrode was positioned in the contralateral ventral hippocampal commissure. Electrode positions were confirmed by postmortem histology. After at least 5 days of recovery, evoked potentials were recorded in awake, freely behaving animals. The electroencephalogram was also recorded to insure that there were no after discharges and that the animals were not asleep. Population spike amplitude was measured between the negative peak and the maximum positive peak of the evoked potential. The

stimulation intensity was adjusted to produce a population spike that was 30% of maximum at the beginning of the experiment, and the evoked potential was tested once every 12 s for at least 40 min. After a 5-min baseline period, primed-burst potentiation was induced during behavioral immobility, with a single stimulus pulse followed 170 ms later by a four-pulse, 200-Hz burst at an intensity that produced a maximal population spike. This procedure was repeated four times: during a baseline session, the next day both 90 and 180 min after injection of CPP (10 mg/kg ip), and again 24 hours after the CPP injection.

19. T. J. McHugh et al., Cell 87, 1339 (1996).

20. R. J. Cole et al., Psychopharmacology 111, 465 (1993); M. P. Pellicano et al., Physiol. Behav. 54, 563 (1993); A. Ungerer et al., Brain Res. 549, 59 (1991).

21. S. Davis et al., J. Neurosci. Methods 75, 75 (1997); R. V. Hernandez et al., Brain Res. 656, 215 (1994); W. C. Abraham and S. E. Mason, ibid. 462, 40 (1988).

22. J. W. Rudy, S. Stadler-Morris, P. Albert, Behav. Neurosci. 101, 62 (1987).

23. K. B. Austin, W. F. Fortin, M. L. Shapiro, Soc. Neurosci. Abstr. 16, 263 (1990).

24. R. U. Muller et al., J. Gen. Physiol. 107, 663 (1996); P. A. Hetherington and M. L. Shapiro, Behav. Neurosci. 107, 434 (1993); R. U. Muller et al., Hippocampus 1, 243 (1991).

25. M. L. Shapiro and C. O'Connor, Behav. Neurosci. 106, 604 (1992); Z. Caramanos and M. L. Shapiro, ibid. 108, 30 (1994).

26. D. M. Bannerman, M. A. Good, S. P. Butcher, M. Ramsay, R. G. M. Morris, Nature 378, 182 (1995); D. Saucier and D. P. Cain, ibid., p. 186.

27. A. Rotenberg, M. Mayford, R. D. Hawkins, E. R. Kandel, R. U. Muller, Cell 87, 1351 (1996); A. Rotenberg, T. Abel, E. R. Kandel, R. U. Muller, Soc. Neurosci. Abstr. 23, 501 (1997); Y. Cho, K. P. Giese, H. Tanila, A. J. Silva, H. Eichenbaum, Science 279, 867 (1998).

28. C. Kentros et al., data not shown.

29. We thank M. Pellan for typing the manuscript. Supported by the Howard Hughes Medical Institute, the National Institute of Mental Health (R01 45923), the NIH (R01 20686), and the National Institute on Aging (T32 AGO 00189).

6 March 1998; accepted 14 May 1998

Edge Effects and the Extinction of Populations Inside Protected Areas

Rosie Woodroffe* and Joshua R. Ginsberg

Theory predicts that small populations may be driven to extinction by random fluctuations in demography and loss of genetic diversity through drift. However, population size is a poor predictor of extinction in large carnivores inhabiting protected areas. Conflict with people on reserve borders is the major cause of mortality in such populations, so that border areas represent population sinks. The species most likely to disappear from small reserves are those that range widely—and are therefore most exposed to threats on reserve borders—irrespective of population size. Conservation efforts that combat only stochastic processes are therefore unlikely to avert extinction.

The contention that small populations are vulnerable to extinction through stochastic processes has a sound theoretical basis in both demography and population genetics (1). Management of small populations has therefore dominated both the theory and practice of conservation biology for nearly 20 years (2). However, most empirical evidence supporting this contention is indirect, because direct measures of size are rarely available for populations that have subsequently become extinct (3).

If small populations are vulnerable, large carnivores should be especially extinction-prone because their trophic position constrains them to living at low population densities. However, carnivore populations are also exposed to strong external pressures because their requirements conflict with those of local people. Where large carnivores survive outside protected

areas, intentional or accidental killing by humans frequently limits their numbers (4). Even within protected areas, conflict with humans is usually the single most important cause of adult mortality (5). Most of this mortality occurs when carnivores range beyond reserve borders (5); such deaths account for proportions of mortality comparable with those known to cause decline in harvested populations of the same species (4, 5). Border areas of reserves may therefore become population sinks. Such sinks will have the greatest impact on overall population dynamics in small reserves with high perimeter:area ratios and in species that range widely and therefore come into frequent contact with reserve borders. In large carnivores, then, both stochastic processes and strong edge effects could contribute to the extinction of isolated populations.

We investigated the relative importance of these two factors by compiling data on population extinctions for 10 species of large carnivores (Table 1). For each species, we chose a geographic region within the species' historic range in which

R. Woodroffe, Department of Zoology, Downing Street, Cambridge CB2 3EJ, UK.
J. R. Ginsberg, Wildlife Conservation Society, Bronx, NY 10460–1099, USA.

*To whom correspondence should be addressed. E-mail: rbw20@cam.ac.uk

Table 1. Results of logistic regressions on the presence and absence of large carnivores in protected areas falling within their historic ranges (7, 8). Wherever possible, data on population densities and home range sizes are taken from the regions for which critical reserve sizes were determined (11). Population density refers to the density of adults, averaged across studies; home range size refers to the mean area used by each adult female (or social group for social species).

Species	Region	No. of reserves	Change in deviance due to		Critical reserve size (km²)†	Population density (adults/100 km²)‡	Home range size (km²)‡
			Reserve age	Reserve size			
Lycaon pictus (African wild dog)	East Africa	46	3.15	26.59***	3606	2.4 (4)	823.1 (12)
Canis lupus (gray wolf)	Western Canada	44	0.0	19.82***	766	1.1 (9)	684.6 (11)
Cuon alpinus (dhole)	India	71	1.69	30.59***	723	10.6 (1)	68.8 (2)
Panthera leo (lion)	East Africa	32	1.39	17.61***	291	16.2 (12)	121.4 (59)
Panthera tigris (tiger)	India, Nepal	154	0.0	39.1***	135	3.6 (3)	16.9 (3)
Panthera uncia (snow leopard)	India, Nepal, Pakistan	30	1.27	21.09***	116	4.6 (6)	29.3 (2)
Panthera onca (jaguar)	Central America	28	0.91	29.98***	69	6.8 (2)	18.8 (5)
Crocuta crocuta (spotted hyena)	East Africa	37	5.14*	20.22***	179	74.5 (6)	34.9 (12)
Ursus americanus (black bear)	California	45	1.48	13.05***	36	58.0 (3)	19.8 (32)
Ursus arctos (brown bear)	Western Canada, Northwest U.S.	54	0.78	18.48***	3981	2.0 (5)	773.8 (36)

*$P = < 0.05$.   ***$P = < 0.0001$.   †The area for which the logistic model predicts a 50% probability of population persistence.   ‡Numbers in parentheses give sample sizes.

suitable habitat has become fragmented. In all of these regions, people kill large carnivores that range outside the protected areas (5). For each region, we identified protected areas that fell within the former geographic range of the species, treating complexes of contiguous reserves as single protected areas (6). We determined the presence or absence of the species in each of these protected areas, using a combination of published and unpublished data (7). Because none of the species has highly specific habitat requirements, and all have experienced range contractions within the last century, their absence from those protected areas that contain suitable habitat can be taken as evidence of local extinction. We excluded areas where evidence indicated that extinction had occurred before the reserves were designated. We recorded the size of each protected area (reserve size) and the time elapsed between the dates when the area was officially designated and when it was surveyed for carnivores (reserve age).

We investigated the relation between reserve size, reserve age, and carnivore extinction, using logistic regression, a standard technique for the analysis of binary data (8). All 10 species were more likely to disappear from small reserves than from larger ones, but extinction was related to reserve age in only one species (Table 1). The statistical effect of reserve size was very strong for all species, but

there was considerable variation in the size of the reserves from which each species had disappeared (Fig. 1). We derived a measure of critical reserve size by using the logistic regression models to predict the area at which populations persisted with a probability of 50%. This measure is analogous to the LD_{50} of a drug, the dose that, administered to experimental subjects, kills exactly half of them. Critical reserve size varied among species by over two orders of magnitude (Table 1).

If probability of extinction is determined primarily by population size, then critical reserve size should be related to average population density, because the size of a population at isolation will be determined by the population density and the area of the reserve. In contrast, if extinction is caused by edge effects, critical reserve size should be related to home range size, as long as reserve shape varies randomly with reserve area. Population density and home range size will not necessarily be correlated with one another, because carnivores that range widely tend to occupy overlapping home ranges (9).

For each species, we collected data from published reports to estimate average population density and average female home range size within the regions for which we investigated population extinction (Table 1). We avoided statistical nonindependence of measures from closely related species by analyzing phylogeneti-
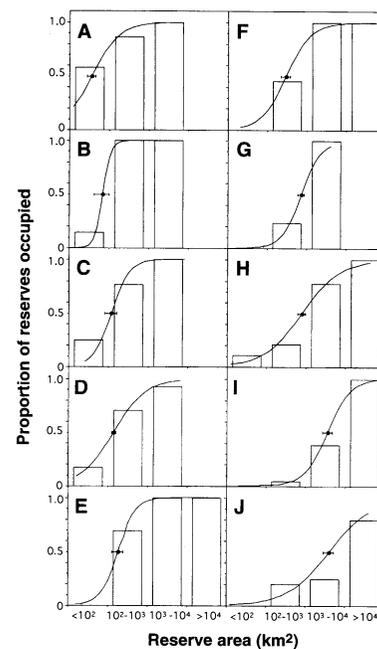

Fig. 1. Proportion of reserves of various sizes in which 10 species of large carnivores have persisted (7). Population persistence is related to reserve area for all species (Table 1). Curves show the probability of persistence predicted by logistic regressions fitted to the binary data (8); filled circles show the critical reserve sizes (±SE) for which the models predict a 50% probability of population persistence. Species: (**A**) black bear; (**B**) jaguar; (**C**) snow leopard; (**D**) tiger; (**E**) spotted hyena; (**F**) lion; (**G**) dhole; (**H**) gray wolf; (**I**) African wild dog; (**J**) grizzly bear.

cally independent contrasts, calculated from a composite phylogeny for the Carnivora (10). All contrasts were calculated with log-transformed data, and all regressions of contrasts on contrasts were forced through the origin.

After controlling for phylogeny, average female home range size was a good predictor of critical reserve size (Fig. 2) ($r^2 = 0.84$, $F_{1,8} = 42.1$, $P < 0.0005$). The effect of population density was much weaker ($r^2 = 0.52$, $F_{1,8} = 8.8$, $P < 0.05$), and disappeared entirely after we controlled for home range size (multiple regression: overall, $F_{2,7} = 20.6$, $P < 0.005$; effect of density, $t = 0.82$, $P > 0.4$; effect of home range size, $t = 4.00$, $P = 0.005$). As expected, contrasts for population density and female home range size were only weakly intercorrelated ($r_8 = -0.69$), partly because some species were social and partly because home range overlap was high in species with large home ranges (9, 11).

These results show that, in a reserve of given size, wide-ranging carnivores are more likely to become extinct than those with smaller home ranges, irrespective of population density. Thus, population size is a relatively poor predictor of extinction among carnivores. Ranging behavior mediates contact with human activity, contact that accounts for a very high proportion of adult mortality in all of these species. Our results therefore indicate that human-induced mortality contributes more to the extinction of populations of large carnivores isolated in small reserves than do stochastic processes. Conservation measures that aim only to combat stochastic processes are therefore unlikely to avert extinction. Instead, priority should be given to measures that seek to maximize reserve size or to mitigate carnivore persecution on reserve borders and in buffer zones.
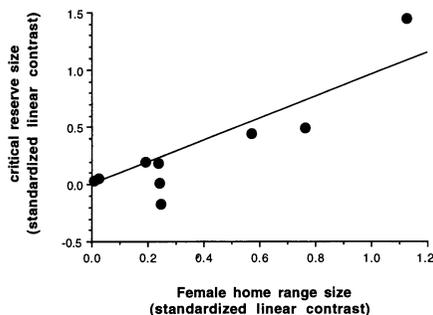

Fig. 2. Relation between phylogenetically independent contrasts in log(critical reserve size) and log(female home range size) calculated for 10 species of large carnivore. $r^2 = 0.84$, $F_{1,8} = 42.1$, $P < 0.005$. The effect remains strong after controlling for the (nonsignificant) effect of population density ($t = 4.00$, $P = 0.005$).

REFERENCES AND NOTES

1. R. Lande, *Science* **241**, 1455 (1988).
2. G. Caughley, *J. Anim. Ecol.* **63**, 215 (1994).
3. W. D. Newmark, *Cons. Biol.* **9**, 512 (1995); but see J. Berger, *ibid.*, **4**, 91 (1990).
4. Several intensive studies of carnivores have shown that deaths caused by people—especially harvesting—increase overall mortality and result in population decline. This impact of harvesting is marked in two species with low fecundity (black and grizzly bears) as well as one with high fecundity (gray wolf). For each species, the proportion of deaths of radio-collared adults caused by people, and sample sizes, are as follows: gray wolf, 79% (97); black bear, 90% (21); grizzly bear, 56% (16). Data sources: gray wolf: W. B. Ballard, J. S. Whitman, C. L. Gardner, *Wildl. Monogr.* **98**, 1 (1987); W. B. Ballard, L. E. Ayres, P. R. Krausman, D. J. Reed, S. G. Fancy, *ibid.*, **135**, 1 (1997); black bear: R. A. Powell, J. W. Zimmerman, D. E. Seaman, J. F. Gilliam, *Cons. Biol.* **10**, 224 (1996); grizzly bear: R. B. Wielgus and F. L. Bunnell, *Biol. Cons.* **67**, 161 (1994).
5. Data from 22 intensive studies of large carnivores in protected areas indicate that 74% of 635 known-cause deaths were directly caused by people. Proportions and sample sizes for each species are as follows: African wild dog, 61% (105); gray wolf, 83% (86); lion, 50% (62); tiger, 67% (3); Iberian lynx, *Felis pardina*, 75% (24); spotted hyaena, 49% (56); black bear, 85% (41); grizzly bear, 89% (258). More detailed data are available at www.sciencemag.org/feature/data/980867.shl. These proportions are comparable with those recorded in populations known to be declining as a result of harvesting (4), indicating that human-caused mortality almost certainly affects the dynamics of populations in protected areas. In 20 of the studies, radiotelemetry was used to locate dead animals, making it unlikely that the data are strongly biased towards deaths caused by people. Most deaths occurred outside reserve borders, caused by legal and illegal hunting as well as road accidents and accidental snaring. Data on grizzly bears also include legal hunting and control of problem animals inside Yellowstone National Park, which together accounted for 130 of 250 deaths recorded there. Quantitative data are not available for jaguars, snow leopards, or dhole, but persecution outside reserves is recorded as a major threat to all three species. Data sources: African wild dog: R. Woodroffe, J. R. Ginsberg, D. W. Macdonald, *The African Wild Dog: Status Survey and Conservation Action Plan* [International Union for the Conservation of Nature and Natural Resources (IUCN), Gland, 1997]; gray wolf: G. J. Forbes and J. B. Theberge, and also D. K. Boyd *et al.*, in *Ecology and Conservation of Wolves in a Changing World*, L. N. Carbyn, Ed. (Canadian Circumpolar Institute, Edmonton, 1995); dhole: J. R. Ginsberg and D. W. Macdonald, *Foxes, Wolves, Jackals and Dogs: An Action Plan for the Conservation of Canids* (IUCN, Gland, 1990); lion: J. Rudnai, *Afr. J. Ecol.* **17**, 85 (1979), C. Packer *et al.*, in *Reproductive Success*, T. H. Clutton-Brock, Ed. (Univ. of Chicago Press, Chicago, 1988); G. B. Schaller, *The Serengeti Lion: A Study of Predator-Prey Relations* (Univ. of Chicago Press, Chicago, 1972); P. E. Stander, *Madoqua* **18**, 1 (1991); tiger: M. E. Sunquist, *Smiths. Contrib. Zool.* **336**, 1 (1981); snow leopard and jaguar: K. Nowell and P. Jackson, *Wild Cats—Status Survey and Conservation Action Plan* (IUCN, Gland, 1996); Iberian lynx: P. Ferreras, J. J. Aldama, J. F. Beltrán, M. Delibes, *Biol. Cons.* **17**, 197 (1992); spotted hyena: H. Hofer, M. L. East, K. L. I. Campbell, *Symp. Zool. Soc. Lond.* **65**, 347 (1993), L. G. Frank, *Anim. Behav.* **34**, 1500 (1986); H. Kruuk, *The Spotted Hyaena* (Univ. of Chicago Press, Chicago, 1972); black bear: E. C. Hellgren and M. R. Vaughan, *J. Wildl. Manage.* **53**, 969 (1989); R. A. Powell, J. W. Zimmerman, D. E. Seaman, J. F. Gilliam, *Cons. Biol.* **10**, 224 (1996); D. L. Garshelis and M. R. Pelton, *J. Wildl. Manage.* **41**, 912 (1981); grizzly bear: J. M. Peek, M. R. Pelton, H. D. Picton, J. W. Schoen, P. Zager, *Wildl. Soc. Bull.* **15**, 160 (1987); S. T. Knick

and W. Kasworm, *ibid.*, **17**, 11 (1989); R. B. Wielgus, F. L. Bunnell, W. L. Wakkinen, P. E. Zager, *J. Wildl. Manage.* **58**, 266 (1994); R. R. Knight and L. L. Eberhardt, *Ecology* **66**, 323 (1985).
6. IUCN, *Protected Areas of the World: A Review of National Systems* (IUCN, Gland, 1992). We included protected areas in categories I, II, and IV defined by the IUCN. These categories include national parks, reserves, and sanctuaries established with the primary aim of protecting wildlife.
7. A summary data set and data sources are available at www.sciencemag.org/feature/data/980867.shl.
8. D. R. Cox, *The Analysis of Binary Data* (Methuen, London, 1970). A model of the form

   p(reserve occupied) = {exp [A + B(log reserve area) + C(log reserve age)]}/{1 + exp [A + B(log reserve area) + C(log reserve age)]},

   where A, B, and C are constants, was fitted to the data by using the Genstat statistical package [Genstat Committee, *Genstat 5 Release 3 Reference Manual* (Clarendon Press, Oxford, UK, 1993)]. Parameters were estimated by maximum likelihood to determine which significantly improved the fit of the model. The effects of reserve age and size were assessed by dropping each in turn from the model, to estimate the contribution of each to total deviance. The resulting changes in deviance are distributed as χ^2, in this case with 1 df.
9. J. W. A. Grant, C. A. Chapman, K. S. Richardson, *Behav. Ecol. Sociobiol.* **31**, 149 (1992).
10. J. Felsenstein, *Am. Nat.* **125**, 1 (1985). Independent contrasts were calculated by using the program CAIC [A. Purvis and A. Rambaut, *Comparative Analysis by Independent Contrasts (CAIC)*, version 2 (Oxford University, Oxford, 1994)], and a composite phylogeny for the Carnivora (O. R. P. Bininda-Emonds, J. L. Gittleman, A. Purvis, unpublished).
11. Full data on population densities and home range sizes, separated by study, are available at www.sciencemag.org/feature/data/980867.shl. Data sources: African wild dog (as in 10); gray wolf: T. K. Fuller, *Wildl. Monogr* **105**, 1 (1989); _____ and L. B. Keith, *J. Wildl. Manage.* **44**, 583 (1980); R. R. Bjorge and J. R. Gunson, *Can. Field Nat.* **103**, 327 (1989); dhole: A. B. Venkataraman, R. Arumugam, R. Sukumar, *J. Zool. Lond.* **237**, 543 (1995); lion: S. Creel and N. M. Creel, *Afr. J. Ecol.* **35**, 83 (1997); K. G. van Ordsol, J. P. Hanby, J. D. Bygott, *J. Zool. London* **206**, 97 (1985); tiger (as in 10); snow leopard: R. Jackson and G. Ahlborn, *Nat. Geog. Res.* **5**, 161 (1989); jaguar: A. R. Rabinowitz and B. G. Nottingham Jr., *J. Zool. London* **210**, 149 (1986); M. E. Tewes and D. J. Schmidly, in *Wild Furbearer Management and Conservation in North America*, M. Novak, J. A. Baker, M. E. Obbard, B. Malloch, Eds. (Ontario Ministry of Natural Resources, Toronto, 1987); spotted hyena: L. G. Frank, *Anim. Behav.* **34**, 1500 (1986); H. Kruuk, *The Spotted Hyaena* (Univ. of Chicago Press, Chicago, 1972); C. Sillero-Zubiri and D. Gottelli, *Afr. J. Ecol.* **30**, 292 (1992); S. R. Creel and N. M. Creel, *Cons. Biol.* **10**, 1 (1996); H. Hofer and M. L. East, *Anim. Behav.* **46**, 547 (1993); black bear: H. J. Novick and G. R. Stewart, *Calif. Fish Game* **68**, 21 (1982); E. C. Hellgren and M. R. Vaughan, *J. Wildl. Manage.* **53**, 969 (1989); D. L. Doancrider and E. C. Hellgren, *ibid.*, **60**, 398 (1996); D. L. Garshelis and M. R. Pelton, *ibid.*, **45**, 912 (1981); A. J. Brody and M. R. Pelton, *Wildl. Soc. Bull.* **17**, 5 (1989); G. B. Kolenosky and S. M. Strathearn, in *Wild Furbearer Management and Conservation in North America*, M. Novak, J. A. Baker, M. E. Obbard, B. Malloch, Eds. (Ontario Ministry of Natural Resources, Toronto, 1987); grizzly bear: R. B. Wielgus and F. L. Bunnell, *Biol. Cons.* **67**, 161 (1994); B. M. Blanchard and R. R. Knight, *ibid.*, **58**, 41 (1991); R. B. Wielgus, F. L. Bunnell, W. L. Wakkinen, P. E. Zager, *J. Wildl. Manage.* **58**, 266 (1994); B. N. McLellan, *Can. J. Zool.* **67**, 1856 (1989); C. Servheen, *J. Wildl. Manage.* **47**, 1026 (1983).
12. We thank S. Durant, L. Frank, G. Mace, J. Robinson, P. Rohani, and K. Rose for valuable comments and discussions.

20 February 1998; accepted 13 May 1998