Animal Conservation (2001) **4**, 345–349 © 2001 The Zoological Society of London Printed in the United Kingdom

Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable

John D. C. Linnell[1], Jon E. Swenson[1,2] and Reidar Andersen[1,3]

[1] Norwegian Institute for Nature Research, Tungasletta 2, 7485 Trondheim, Norway
[2] Department of Biology and Nature Conservation, Agricultural University of Norway, PO Box 5014, 1432 Ås, Norway
[3] Zoology Department, Norwegian University of Science and Technology, 7491 Trondheim, Norway

(Received 12 September 2000; accepted 11 June 2001)

Abstract

In a recent analysis Woodroffe (2000) found a positive relationship between historical patterns of large carnivore extinction probability and human population density. However, much of the data in this analysis came from a period when carnivore extermination was a management objective. In order to explore the hypothesis that large carnivores can persist at high human densities when the management regime is more favourable we have repeated the analysis using up-to-date data from North America and Europe. In North America we found that large carnivore populations have increased after favourable legislation was introduced, despite further increases in human population density. In Europe we found no clear relationship between present carnivore distribution and human population density. We therefore believe that the existence of effective wildlife management structures is more important than human density *per se*.

INTRODUCTION

In our modern and crowded world, large carnivores are among the most challenging taxonomic groups to conserve (Mech, 1995). Their massive area requirements and predatory behaviour (on both wild prey and livestock) lie at the core of the problem (Nowell & Jackson, 1996). In addition, their populations have been dramatically reduced during the last 200 years. However, their decline has not been uniform throughout the world, and while some populations have been exterminated, others have survived to a far greater degree. In a recent analysis of historic trends, Woodroffe (2000) attempted to explain some of this variation by examining the relationship between large carnivore extinction probability and increasing human population density. For a variety of species, Woodroffe found a clear positive relationship between human density and extinction probability. However, we believe that while being a fair analysis of past processes her analysis does not present an accurate picture of the ability for large carnivores to persist in the modern world under favourable management regimes. Instead, against a background of European experience and an examination of more modern North American data (which were not covered by Woodroffe), we present the thesis that large carnivore persistence is more adequately explained by management policy, and the enforcement of this policy, than human population density *per se*.

All correspondence to: John Linnell. Tel: ++ 47 73 801 442; Fax: ++ 47 73 801 401; E-mail: john.linnell@ninatrd.ninaniku.no

RECENT TRENDS IN NORTH AMERICAN LARGE CARNIVORE POPULATIONS

The North American extinction data used by Woodroffe (2000) stem from the late 1800s and early 1900s. During this entire period the widespread social agenda, and politically sanctioned policy, was to eradicate large carnivores (Mech, 1970; Brown, 1983; chapters in Novak *et al*., 1987). Bounties were offered at various times by county, state and federal administrations. In addition, large amounts of federal money were used to support professional hunters who used all available methods (e.g., traps, poison, aerial hunting) to kill carnivores. During the same time period, there was widespread conversion of forest habitats to farmland, and decimation of the prey base of native ungulates on which large carnivores depend. As human population size also correlates with time, the data analyzed by Woodroffe (2000) describe the progressive success of this extermination policy, and the temporal progression of immigrant expansion into relatively unsettled territory, rather than a simple causal density-dependent relationship between human density and carnivore extinction. Woodroffe's critical human density appears to be a measure of the effort that humans must make in order to exterminate large carnivores when they are trying. Therefore we believe that it is not

directly relevant to the discussion about how to conserve large carnivores when we actually try.

If our hypothesis on the role of management policy is correct, large carnivore populations should have stabilized or recovered once policy objectives changed, despite the fact that human density remained stable or increased further. Official policy towards all predators, including large carnivores, began changing after the 1940s, but the most dramatic changes occurred during the early 1970s (Novak *et al*., 1987, and references therein). The indiscriminate use of toxicants for carnivore control was banned in the United States in 1972, and wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) were placed on the endangered species list (in the lower 48 states) in 1974 and 1975, respectively. Similarly, bounties were removed from wolves in the various Canadian provinces between 1949 (Saskatchewan) and 1975 (Northwest Territories). By the mid-1970s wolves, grizzly bears and cougars (*Puma concolor*) were all either protected or managed as harvestable game species (game or furbearer designations) throughout Canada and the United States (Novak *et al*., 1987, and references therein).

In the subsequent 25 years, there have been no further extinctions of these three species in their range states/provinces (Table 1). Although there have been some local declines, these either have been due to planned population reductions, or were reversed after the decline was detected. In fact, most populations have expanded. Wolves have naturally expanded from northeastern Minnesota (the only area where they persisted in the lower 48 states) to recolonize central Minnesota, upper Michigan and parts of Wisconsin and North Dakota. In addition, northern Montana has been recolonized from Alberta (Mech, 1995). In addition, the deliberate reintroduction of wolves into formerly occupied habitats in Idaho and the Greater Yellowstone ecosystem has been a success (Bangs *et al*., 1998), and a new reintroduction is underway in the southwestern states (Parsons, 1998). Grizzly bear populations in Alaska and Canada remain secure, and even the five remnant populations in the lower 48 states have generally held their own (Servheen, Herrero & Peyton, 1999). Augmentation of the grizzly bear population in the Cabinet–Yaak area of Montana has been carried out, and a reintroduction into the Selway–Bitteroot area on the Idaho–Montana border is being planned (Servheen *et al*., 1999). Wildlife managers in 15 states and provinces have reported that their cougar populations are either stable or increasing, including the isolated population of cougars in Florida (reports in Paldey, 1997). This is all despite the fact that the human population of North America has almost quadrupled since 1900 (Woodroffe's survey date) and has increased by 25% since 1975 when the modern era of conservation-orientated large carnivore management began. Many of these states (Table 1) have human populations well above Woodroffe's cut-off densities (4–14 people km^{-2}), and wolf recovery plans are being seriously evaluated for northeastern states like New York which has 148 people per km^2 (Mladenoff & Sickley, 1998).

Table 1. Present trends in wolf and cougar populations in North American states in relation to present human population density. Human population densities are for the year 2000 (US Census Bureau). Carnivore population trends are indicated by arrow symbols (↗ = increasing, → = stable, ↘ = decreasing)

State/province	Human density	Cougar[1]	Wolf[2]
Alaska	0.4		→
Alberta	4.1	↗	→
Arizona	16.2	→	
BC	3.9	↗	↗
California	82.1	↗	
Colorado	15.1	↗	
Florida	108.1	→	
Idaho	5.8	↗	
Labrador	1.4		→
Manitoba	1.7		→
Michigan	67.0		↗
Minnesota	23.2		↗
Montana	2.3	↗	↗
Nevada	6.4	↗	
New Mexico	5.5	↗	
NWT[3]	0.02		→
Ontario	10.0		↗
Oregon	13.3	↗	
Quebec	4.6		↗
Saskatchewan	1.5		→
Texas	29.6	↗	
Utah	10.0	↗	
Washington	33.4	↗	
Wisconsin	37.3		↗
Wyoming	1.9	↗	
Yukon	0.06		→

[1] Source = state-by-state survey from fifth mountain lion workshop in 1996 (Paldey, 1997).
[2] Source = Hayes & Gunson, 1995; Stephenson *et al*., 1995; Thiel & Ream, 1995; figures generally include up to 1992.
[3] Trend does not include High Arctic areas where data are lacking.

CARNIVORE PERSISTENCE IN EUROPE AT HIGH HUMAN DENSITY

If large carnivore persistence is simply linked to human population density *per se*, we should expect to find a similar relationship between carnivore persistence and human population density in an area not considered by Woodroffe. To examine this issue we collated data on the past distribution and present status of brown bear (*Ursus arctos*), wolf and Eurasian lynx (*Lynx lynx*, the ecological equivalent of a cougar) in Europe from a series of action plans, recently published by the Council of Europe (Boitani, 2000; Breitenmoser *et al*., 2000; Swenson *et al*., 2000) and the IUCN (Nowell & Jackson, 1996; Servheen *et al*., 1999). Additional status updates presented at a meeting of the 'Group of Experts on Large Carnivores to the Council of Europe's Bern Convention' in Oslo in June 2000 were included in some cases. We considered countries to be former-range states if large carnivore populations had persisted into the early 1800s (this excludes cases like wolf extinction from Britain and Ireland that occurred in the 1600s for example). Extinction was defined if a given species did not occur in a consistently reproducing status for a period of at least some decades (Table 2). In order to test for the ability of large carnivores to persist under modern management regimes we repeated the analysis using present

Table 2. Present trends in large carnivore populations in European countries in relation to present human population density. P? = reproducing population present but trend is uncertain; T = only transient individuals present; E = extinct; NP = never present. Human population densities are for the year 2000 (US Census Bureau). Carnivore population trends are indicated by arrow symbols (↗ = increasing, → = stable, ↘ = decreasing)

Country	Human density (km^{-2})	Lynx[1]	Bear[2]	Wolf[3]
Albania	121.40	P?	→	↗
Austria	96.97	T	↗	E
Bosnia	75.02	P?	P?	↘
Bulgaria	70.30	E	↘	→
Croatia	75.73	→	→	↗
Czech Republic	130.30	→	T	↗
Estonia	31.73	→	→	→
Finland	15.33	↗	↗	↗
France	107.98	↗	→	↗
Germany	232.12	↗	E	T
Greece	80.35	P?	↘	→
Hungary	108.99	T	E	T→
Italy	191.33	T	→	↗
Latvia	37.76	→	→	→
Lithuania	55.54	→	T	↗
Macedonia (FYROM)	79.37	P?	→	↗
Moldova	131.48	E	E	→
Norway	13.82	→	↗	↗
Poland	123.59	→	→	↗
Portugal	109.12	NP	E	→
Romania	94.36	→	(↘)[4]	↗
Slovakia	110.29	↘	↗	→
Slovenia	95.21	→	→	↗
Spain	79.24	NP	↘	↗
Sweden	19.73	↗	↗	↗
Switzerland	175.89	→	E	T↗
Ukraine	81.42	P?	↘	→
Yugoslavia	104.36	P?	P?	P?

[1] Source = Breitenmoser *et al*., 2000; figures are for 1998.
[2] Source = Swenson *et al*., 2000; figures are for 1998.
[3] Source = Boitani, 2000; figures are for 1998.
[4] Reducing the brown bear population is currently a management goal in Romania.

distributions of reproductive populations (including the results of both natural recolonization and reintroduction).

There was some subjectivity associated with classifying a population within a national border as simply present or extinct, because many populations straddle international borders and are in a dynamic state. This was especially true for Norway, as wolves only recolonized in 1998 (represented by only three packs that use Norwegian territory exclusively in 2000) and no reproducing female bears exclusively use Norwegian territory (Swenson, Sandegren & Söderberg, 1998). As Norway has by far the lowest human population density in mainland Europe, the classification of its wolf and bear populations can have a dramatic effect on the analysis. Therefore, we carried out separate analyses where these populations were considered as either present or extinct, respectively. Human population densities were taken from the estimated present densities (year 2000) by the United States Census Bureau. Although some countries' populations may have grown at slightly different rates during the last two centuries, we believe that the relative rankings should be unchanged, and present human density is directly relevant to the analysis for persistence at the present time.

The only species showing a significant relationship between human population density and historical extinction since the early 1800s was the Eurasian lynx (Tables 2 and 3). This probably reflects the greater vulnerability of lynx to human influences on their ungulate prey base rather than disproportionate human persecution. Lynx are strictly carnivorous and therefore cannot survive in the absence of prey species; wolves and bears are better able to survive on garbage and plants, respectively. With regard to present coexistence with humans, lynx showed no relationship to human density, owing to their successful reintroduction and recolonization in many countries in central Europe. Although the present status of both wolves and bears appeared to show a relationship with human density, this was due to the influence of Norway as an outlying data point (Table 3). If Norwegian wolf and bear populations were included in the analysis as functionally extinct, then there was no significant relationship between human density and carnivore presence.

There is no doubt that Europe's large carnivores have been greatly reduced owing to human activities during past centuries. Direct persecution, destruction of their prey base and deforestation have all led to dramatic reductions in distribution and numbers (Boitani, 1995; Breitenmoser, 1998). Large carnivores were driven to extinction in many countries, often early in historic or even prehistoric times. However, the results from our analysis show that, in general, there are few consistent relationships between human population density and large carnivore extinction in Europe. In addition, the critical densities are far higher than those found by Woodroffe for North American large carnivores. Why is this?

We believe that it is due to two factors. First, it is important to remember that Europeans have shared their continent with large carnivores for around 30,000 years.

Table 3. Logistic regression analysis of large carnivore extinction in European countries with respect to human population density. 'Past extinction' includes countries where the species became extinct for a period of at least several decades after 1800. 'Present status' is based on the data in Table 2, and includes the results of population persistence, recolonization and reintroduction. The later analysis has been presented with and without Norway, as the country's low population density gives it a strong effect on the analysis, and the status of wolves and bears is undergoing rapid change

	N	c^2	*P*	Mean human density at extinction	Mean human density at persistence
Lynx					
Past extinction	26	9.0	0.003		
Present status	26	0.2	0.677	94.0 ± 32.8	94.7 ± 55.1
Brown bear					
Past extinction	28	1.1	0.3		
Present status	28	4.8	0.03	135.5 ± 61.2	83.4 ± 42.4
Present status (Norway set as extinct)	28	0.4	0.52		
Wolf					
Past extinction	28	0.01	0.904		
Present status	28	6.7	0.01	168.3 ± 67.9	85.8 ± 41.7
Present status (Norway set as extinct)	28	0.08	0.773		

This long-term overlap has led to a relatively high degree of coexistence, for example with wolves exploiting anthropomorphic food sources when wild prey are absent (Vos, 2000), and with shepherds adopting effective methods of guarding their livestock (Coppinger & Schneider, 1995). The second factor is clearly one of tradition, which is expressed through management regulation (Boitani, 1995). Royal decrees to regulate hunting of bears date back to the 1600s in some cases, and most countries were managing bears as game species by the early- to mid-1900s. There is no doubt that the concept of hunting large carnivores as game species is far older in Europe than in North America and contributed greatly to their persistence. In addition, despite the very high human densities in Europe today (Table 2), the historic declines in large carnivore numbers appear to have been reversed with only a few exceptions. Large carnivore population trends in most countries are stable or increasing, and intensive conservation efforts are underway to reverse the slow declines occurring in a few areas.

One example that clearly shows the importance of management policy is that of brown bears in Scandinavia (Swenson *et al*., 1995). Both countries have low human population densities (14 km^{-2} in Norway, 20 km^{-2} in Sweden). Bounties on bears were introduced early (1733 in Norway, 1647 in Sweden). As a result, bear populations were rapidly reduced in both countries. However, management policy diverged in the late 1800s. Bounties were removed in Sweden in 1893, and increasing levels of protection were phased in from 1909. This led to such an increase that managed hunting could begin in 1943. Today there is a population of about 1000 bears, that is still increasing despite providing an annual harvest of 50 bears (Sandegren & Swenson, 1997). In contrast, despite phasing out the state bounty in 1930 in Norway, unregulated killing was still permitted up until 1972, when bears were finally given protection. By this time they were functionally extinct (Swenson *et al*., 1995, 1998). Recolonization from Sweden, Russia and Finland is presently allowing a slow recovery of the Norwegian population.

CONCLUSIONS

In conclusion, the data support our hypothesis that patterns of large carnivore extinction and persistence in Europe and North America are more adequately explained by management policy and its enforcement than by human population density. We therefore predict that human density and carnivore density interact differently in two phases of the development of wildlife management structures. First, where there is no effective regulation of human behaviour, weapons (and poison) are available, and a rapid period of human expansion occurs into areas where resource exploitation is not controlled, large carnivore extinction should be related positively to human density (the 'frontier' phase). This is mediated by a combination of habitat change, destruction of prey base and direct persecution. This situation broadly corresponds to North America up until the mid-1900s, and much of the developing world today. Woodroffe's (2000) analysis of North American data has clearly shown how large carnivore extermination can be achieved (if desired) even at very low human densities. Second, where there is effective regulation of human behaviour and established human populations in areas where resource exploitation is regulated, there should be no strong correlation between human density and carnivore extinction (the 'stabilised' or 'wildlife management' phase). This corresponds to most of Europe and North America today. In this phase, large carnivore recovery into remaining habitat can occur, through either natural recolonization or planned reintroduction. The European experience shows how brown bears, lynx and wolves can survive at high human densities.

The important implication of our results is that large carnivore conservation requires the rapid establishment of effective wildlife management and enforcement structures that either make protection effective or regulate harvest of both large carnivores and their prey at sustainable levels. Of course, achieving this in the developing world requires a whole range of measures, like slowing human population growth, and fostering sustainable socio-economic development. The point is that large carnivore conservation is possible at high human density, and that even wilderness protection is no guarantee of persistence (Woodroffe & Ginsberg, 1998). European and North American experience clearly shows that large carnivores and their prey can persist within many heavily modified habitats (though not all) at high human densities and even where both predators and their prey are being harvested. In the face of the pressures on wilderness areas today, this is extremely good news for large carnivores (Linnell, Swenson & Andersen, 2000). Implementation of such a policy requires an urgent building of bridges between the academic field of conservation biology and the hands-on field of wildlife management.

Acknowledgements

We would like to thank Hans C. Pedersen, Henrik Brøseth, John Odden and Erling J. Solberg for constructive input into this discussion.

REFERENCES

Bangs, E. E., Fritts, S. H., Fontaine, J. A., Smith, D. W., Murphy, K. M., Mack, C. M. & Niemeyer, C. C. (1998). Status of gray wolf restoration in Montana, Idaho, and Wyoming. *Wildl. Soc. Bull.* **26**: 785–798.

Boitani, L. (1995). Ecological and cultural diversities in the evolution of wolf–human relationships. In *Ecology and conservation of wolves in a changing world:* 3–12. Carbyn, L. N., Fritts, S. H. & Seip, D. R. (Eds). Edmonton, Alberta: Canadian Circumpolar Institute.

Boitani, L. (2000). Action plan for the conservation of the wolves in Europe (*Canis lupus*). *Council of Europe, Nature and Environment* **113**: 1–86.

Breitenmoser, U. (1998). Large predators in the Alps: the fall and rise of man's competitors. *Biol. Conserv.* **83**: 279–289.

Breitenmoser, U., Breitenmoser-Würsten, C., Okarma, H., Kaphegyi,

T., Kaphegyi-Wallmann, U. & Müller, U. M. (2000). Action plan for the conservation of the Eurasian lynx in Europe (*Lynx lynx*). *Council of Europe, Nature and Environment* **112**: 1–69.

Brown, D. E. (1983). *The grizzly in the southwest*. Norman: University of Oklahoma Press.

Coppinger, R. & Schneider, R. (1995). Evolution of working dogs. In *The domestic dog:* 21–47. Serpell, J. (Ed.). Cambridge: Cambridge University Press.

Hayes, R. D. & Gunson, J. R. (1995). Status and management of wolves in Canada. In *Ecology and conservation of wolves in a changing world:* 21–34. Carbyn, L. N., Fritts, S. H. & Seip, D. R. (Eds). Edmonton, Alberta: Canadian Circumpolar Institute.

Linnell, J. D. C., Swenson, J. E. & Andersen, R. (2000). Conservation of biodiversity in Scandinavian boreal forests: large carnivores as flagships, umbrellas, indicators, or keystones? *Biodiv. Conserv*. **9**: 857–868.

Mech, L. D. (1970). *The wolf: the ecology and behavior of an endangered species*. New York: American Museum of Natural History.

Mech, L. D. (1995). The challenge and opportunity of recovering wolf populations. *Conserv. Biol*. **9**: 270–278.

Mladenoff, D. J. & Sickley, T. A. (1998). Assessing potential gray wolf restoration in the northeastern United States: a spatial prediction of favorable habitat and potential population levels. *J. Wildl. Mgmt*. **62**: 1–10.

Novak, M., Baker, J. A., Obbard, M. E. & Malloch, B. (1987). *Wild furbearer management and conservation in North America*. Toronto: Ontario Ministry of Natural Resources.

Nowell, K. & Jackson, P. (1996). *Wild cats: status survey and action plan*. Gland, Switzerland: IUCN.

Paldey, W. D. (1997). *Proceedings of the fifth mountain lion workshop*. San Diego, CA: Southern California Chapter, The Wildlife Society.

Parsons, D. R. (1998). 'Green fire' returns to the southwest: reintroduction of the Mexican wolf. *Wildl. Soc. Bull*. **26**: 799–807.

Sandegren, F. & Swenson, J. E. (1997). *Björnen: viltet, ekologin och människan*. Uppsala: Svenska Jägareförbundet.

Servheen, C., Herrero, S. & Peyton, B. (1999). *Bears: status survey and conservation action plan*. Cambridge: IUCN Publications.

Stephenson, R. O., Ballard, W. B., Smith, C. A. & Richardson, K. (1995). Wolf biology and management in Alaska, 1981–1992. In *Ecology and conservation of wolves in a changing world:* 43–54. Carbyn, L. N., Fritts, S. H. & Seip, D. R. (Eds). Edmonton, Alberta: Canadian Circumpolar Institute.

Swenson, J. E., Gerstl, N., Dahle, B. & Zedrosser, A. (2000). Action plan for the conservation of the brown bear in Europe (*Ursus arctos*). *Council of Europe, Nature and Environment* **114**: 1–69.

Swenson, J. E., Sandegren, F. & Söderberg, A. (1998). Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *J. Anim. Ecol*. **67**: 819–826.

Swenson, J. E., Wabakken, P., Sandegren, F., Bjärvall, A., Franzén, R. & Söderberg, A. (1995). The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. *Wildl. Biol*. **1**: 11–25.

Thiel, R. P. & Ream, R. R. (1995). Status of the gray wolf in the lower 48 United States to 1992. In *Ecology and conservation of wolves in a changing world:* 59–62. Carbyn, L. N., Fritts, S. H. & Seip, D. R. (Eds). Edmonton, Alberta: Canadian Circumpolar Institute.

Vos, J. (2000). Food habits and livestock depredation of two Iberian wolf packs (*Canis lupus signatus*) in the north of Portugal. *J. Zool. (Lond.)* **251**: 457–462.

Woodroffe, R. (2000). Predators and people: using human densities to interpret declines of large carnivores. *Anim. Conserv*. **3**: 165–173.

Woodroffe, R. & Ginsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. *Science* **280**: 2126–2128.