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Predators and people: using human densities to interpret declines of large carnivores

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Abstract

The current extinction crisis is caused primarily by human impacts upon wild populations. Large carnivores are especially sensitive to human activity; because their requirements often conflict with those of local people, predators have been actively persecuted in most regions of the world. In this paper, the impact of people upon predators is analysed by relating local carnivore extinctions to past and projected human population densities. There are strong associations between high human density and the loss of carnivore populations from a region. Interspecific variation in ability to survive at high human densities probably reflects species' ability to adapt to human-modified habitats. However, regional and temporal variation in individual species' sensitivity to human density is more likely to reflect the activities of local people than the phenotypes of local carnivores. Local culture, government policy and international trade all influence human attitudes to predators and, therefore, the impact of people upon carnivore populations. The importance of these factors may mean that extinction risks for carnivores will continue to increase, even though human population growth is projected to decelerate during the new millennium. This points to an urgent need for techniques to resolve conflicts between people and predators at either the local or landscape level.

INTRODUCTION

The expansion of human populations underlies many of the species declines and extinctions currently occurring world-wide. Human activities modify people's surroundings in a variety of ways; as people become more numerous, this process creates new environments that are hostile to many wild species. For this reason, many conservation programmes aim, ultimately, to mitigate human impact upon wildlife.

Large carnivores are likely to be especially sensitive to the growth of human populations. Because they may kill livestock and even, occasionally, people, carnivores are tolerated by few human societies. Persecution is widespread, ranging in scale from the occasional poisoning of hyaenas by African pastoralists, to the government-sponsored eradication of wolves across the contiguous United States of America in the 19th and 20th centuries. As a result of such conflicts, killing by people remains the greatest threat to the persistence of many large carnivores (Woodroffe & Ginsberg, 1998). Even nominally protected populations may be at risk: contact with people at reserve borders is a major cause of mortality, which may cause local population extinctions where reserves are too small to enclose the home ranges of the animals that inhabit them (Woodroffe & Ginsberg, 1998).

These observations indicate that future conservation efforts depend upon understanding the interactions between predators and people. In this paper, I relate past carnivore declines to the growth of human populations, in order to investigate the circumstances that predispose some carnivore populations to local extinction. In addition, I use projections of human population growth to predict future carnivore declines.

METHODS

Carnivore declines were investigated using a combination of historical and contemporary data. For each species, one or more regions were chosen in which decline had occurred. For each region, a point in time was selected when carnivore populations had disappeared from some parts of the region, but had persisted in others. Data were collated from the literature to allow a comparison of the distribution of predators and people across regional sub-divisions (states, districts or counties) at these times; an example is given in Fig. 1.

The persistence of carnivore populations was com-

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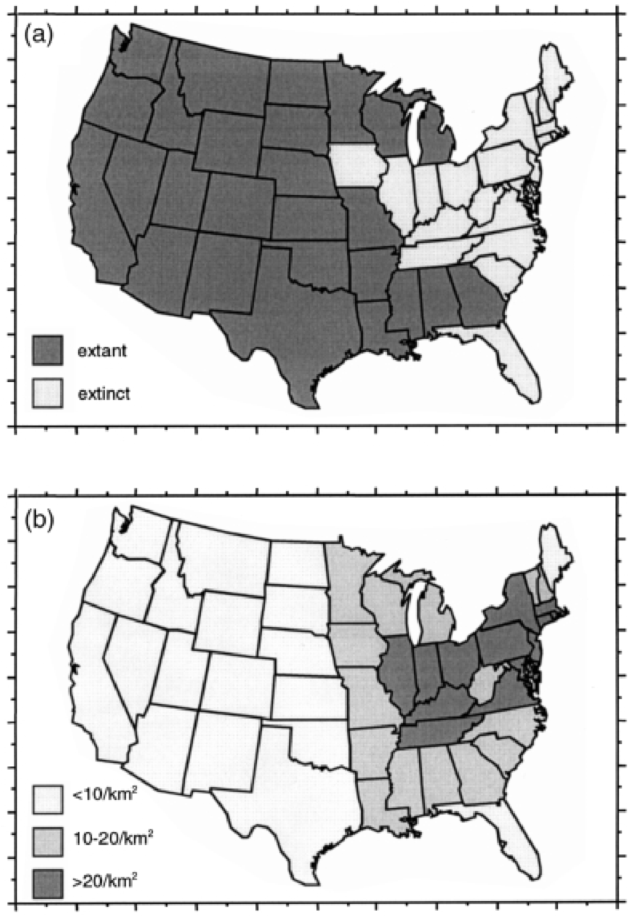

Fig. 1. Distribution of wolves and people across the coterminous United States of America in 1900. (a) States in which wolves had been eradicated (light shading) and those in which one or more populations persisted (heavy shading). Heavy shading does not imply that wolves were continuously distributed across the entire state. Data from Young & Goldman (1944). (b) Human population density on a statewide basis; some states categorized as having densities of >20 people/km^2 contained as many as 200 people/km^2. Data from U.S. Census Bureau (1999*b*).

pared with local human density using logistic regression, a standard technique for the analysis of binary data (fig. 2: Cox, 1970). A model of the form:

p(carnivores present) = (exp(A + B(log human density)))/(1 + exp (A + B(log human density)))

where A and B are constants, was fitted to the data using the statistical package Genstat (Genstat-Committee, 1993). Parameters were estimated using maximum likelihood to determine the best fit of the model. The statistical effect of log(human density) was determined by estimating its contribution to total deviance; the resulting changes in deviance are distributed as χ^2, in this case with one degree of freedom.

Where logistic regressions indicated a significant association with human density, the regression models were used to calculate a ‘critical human density’, at which local population extinction was predicted to occur with a probability of 50%. This estimate is analagous to a measure of LD_{50} (lethal dose$_{50}$), the dose of a drug that kills exactly 50% of experimental subjects. Upper and lower estimates of critical human density were derived from the standard error of the probability of extinction, estimated during the process of model fitting.

For some species, it was posible to derive additional, independent estimates of critical human density using historical data. Where local extinction dates were known, census data were used to determine local human density at that time; averaging these measures gave an alternative measure of the human density associated with carnivore population extinction. Where both measures were available, these independent estimates fell within the upper and lower estimates of critical density calculated from logistic regressions (Table 1), suggesting that the regression method gives a realistic prediction of critical human density.

Where logistic regressions indicated a significant association with human density, regional critical human densities were used to predict future local extinctions. Combining baseline local human densities (used in the calculation of critical human densities) with U.S. government projections of national human population growth for the countries concerned (U.S. Census Bureau, 1999*a*), future human densities were projected within each state, district or county, for each decade until 2050. Nationwide projections were used because more local projections were rarely available. This approach necessarily ignored processes such as urbanization and migration between districts or between nations; the projections of local human density are therefore inaccurate, and the results must be interpreted with caution. Carnivore populations were assumed to become locally extinct when projected human density exceeded the critical thresholds shown in Table 1. Upper and lower estimates of extinction rates were calculated using the upper and lower estimates of critical density described above.

The accuracy of projected declines was tested using historical data. For North American species, critical human densities around 1900 were estimated. These estimates were then used to predict extinctions during the 20th century, using observed rates of human population growth (U.S. Census Bureau, 1999*b*).

RESULTS

Relationships between human density and carnivore extinctions

The results of the logistic regressions are presented in Table 1. For most of the species tested, local extinction was significantly associated with high human population density (Table 1, Fig. 2), and trends were in this direction for all species.

For the North American species (wolf, mountain lion and grizzly bear), two independent estimates of critical human density could be calculated from the same region, using different methods. These estimates are broadly comparable (Table 1), suggesting that both methods give

Table 1. Logistic regressions of carnivore persistence upon human population density

Species	Location	Date	Change in deviance	*n*	Critical human density*	Mean density at extinction†	Data sources
African wild dog *Lycaon pictus*	Kenya	1990	29.3***	41 districts	6.3 people/km^2 (4.1 – 9.6)	–	1,2
	Southern Africa	1996	22.1***	48 districts	0.7 people/km^2 (0.5 – 1.0)	–	1,3,4,5
Wolf *Canis lupus*	United States of America	1900	36.5***	49 states	13.0 people/km^2 (11.0 – 15.3)	13.5 people/km^2 (11.2 – 15.8)	6,7
Cheetah *Acinonyx jubatus*	Kenya	1986	11.7***	24 districts	16.5 people/km^2 (9.8 – 27.2)	–	2
	India	1901	0.42	10 states	not calculated	120 people/km^2 (88.4 – 150.8)	8,9,10
Lion *Panthera leo*	India	1901	1.27	8 states	not calculated	26.0 people/km^2 (13.4 – 38.6)	9,10,11,12
Mountain lion *Felis concolor*	United States of America	1900	36.1***	43 states	11.7 people/km^2 (9.7 – 14.1)	13.3 people/km^2 (10.7 – 15.9)	7,13
Jaguar *Panthera onca*	Brazil	1987	18.1***	21 states	17.3 people/km^2 (12.8 – 23.3)	–	14,15
Leopard *Panthera pardus*	Kenya	1986	8.4**	41 districts	958 people/km^2 (497 – 1857)	–	2,16
Spotted hyaena *Crocuta crocuta*	Kenya	1990	22.6***	36 districts	79.5 people/km^2 (57.0 – 111)	–	2,17
Grizzly bear *Ursus arctos*	United States of America	1910	7.5*	16 states	4.2 people/km^2 (3.1 – 5.7)	4.2 people/km^2 (2.6 – 5.8)	7,18
Black bear *Ursus americanus*	United States of America	1970	2.6	48 states	not calculated	–	7,19

*Human population density at which logistic regression predicts a 50% probability of carnivore extinction (presented ±SE); calculated only where regression models showed a statistically significant effect of human density.
†Mean human population density in the year in which extinction occurred (±SE).
***P<0.001; **P<0.005; *P<0.01.
Sources: 1, Fanshawe *et al.* (1997); 2, Hamilton (1986*a*); 3, Central Statistics Office (1992); 4, National Planning Commission (1992); 5, Central Statistics Office, Zimbabwe (1992); 6, Young & Goldman (1944); 7, U.S. Census Bureau (1998); 8, Divyabhanusinh (1995); 9, India Census Commissioner (1901); 10, India Census Commissioner (1941); 11, Pocock (1930); 12, Talbot (1959); 13, Nowak (1976); 14, Swank & Teer (1989); 15, Government of Brazil (1998); 16, Hamilton (1986*b*); 17, Mills & Hofer (1998); 18, McCracken (1957); 19, Herrero (1972).

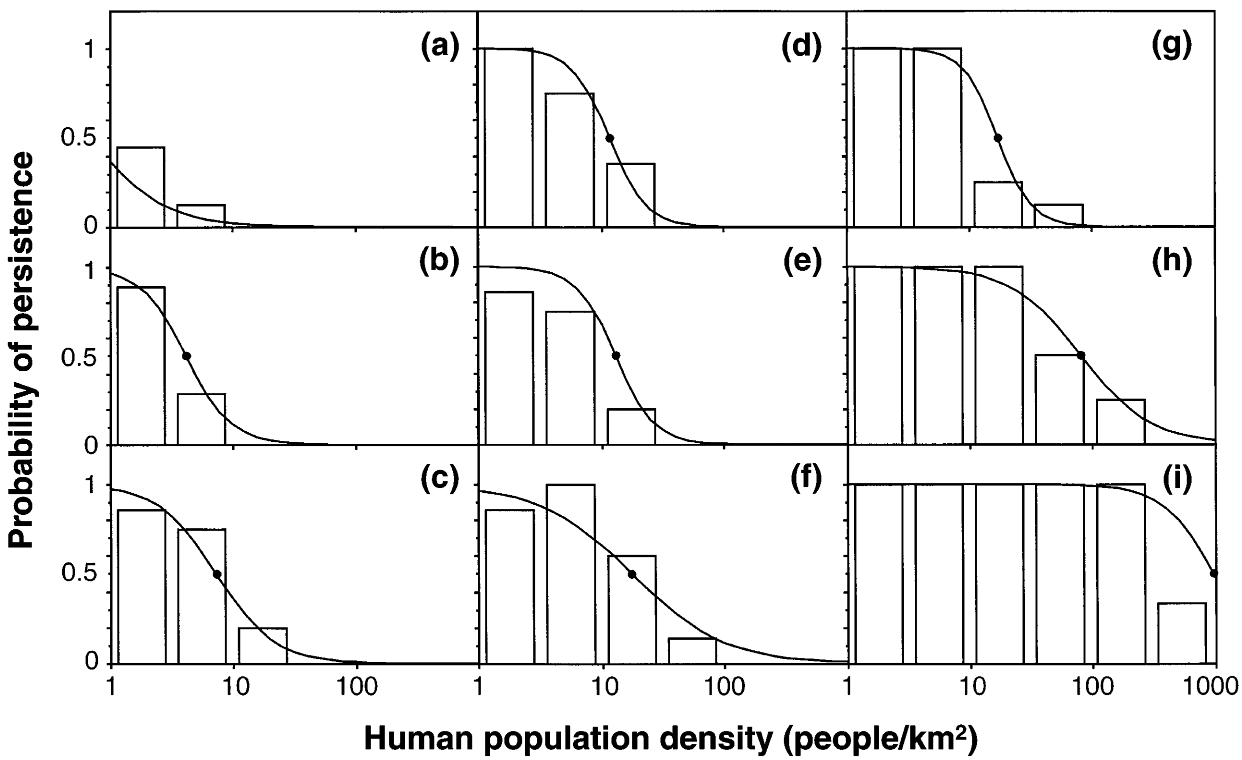

Fig. 2. Relationships between human density (measured on a logarithmic scale) and carnivore persistence. Each histogram gives the proportion of states, counties or districts still occupied by the carnivore species; curves show the logistic regression models fitted to the binary data. Solid circles indicate the human densities at which the regression models predict a 50% probability of local extinction. Statistical analyses and data sources are presented in Table 1. Species and locations: (a) African wild dog, southern Africa; (b) grizzly bear, USA; (c) African wild dog, Kenya; (d) mountain lion, USA; (e) wolf, USA; (f) cheetah, Kenya; (g) jaguar, Brazil; (h) spotted hyaena, Kenya; (i) leopard, Kenya.

a realistic picture of the human density at which carnivore extinction occurs.

For two species (African wild dog and cheetah), two independent estimates of critical human density could be calculated from different regions (for cheetahs these were calculated using different methods). These independent estimates differ substantially (Table 1), perhaps indicating regional variation in the species' sensitivity to human activity.

Projecting future declines

Projected declines are shown in Fig. 3. Note that most species are predicted to decline fairly slowly, and then stabilize; this reflects the stabilization of human populations projected to occur within the next century (U.S. Census Bureau, 1999*a*).

Fig. 4 compares the rates of decline observed in North American carnivores with those predicted on the basis of recorded human population growth. Wolves and mountain lions declined more rapidly than predicted in the early part of the 20th century. Wolf populations are now recovering (Mech, 1995), despite continuing growth of the human population. These inaccuracies in the predictive power of human population growth suggest that the projections shown in Fig. 3 may also be inaccurate, and they are presented for illustrative purposes only. Possible explanations are outlined in the Discussion, below.

DISCUSSION

For most of the species considered here, local extinctions are associated with growing human populations. As human densities continue to rise, carnivores can be expected to decline further. Furthermore, since some carnivores' wide-ranging behaviour places even protected populations in contact with human activities (Woodroffe & Ginsberg, 1998), declines may be seen inside, as well as outside, national parks and reserves. Resolving conflicts between people and predators is vital, therefore, to avert future extinctions.

For three species, no significant relationships could be detected between high human density and extinction. For two of the species (lions and cheetahs in India), this could be due to small sample sizes. For the other species (the black bear), however, it may be a result of the geographical scale for which data were collated. Black bear decline was investigated at the level of the state, on a scale measured in tens of thousands of square

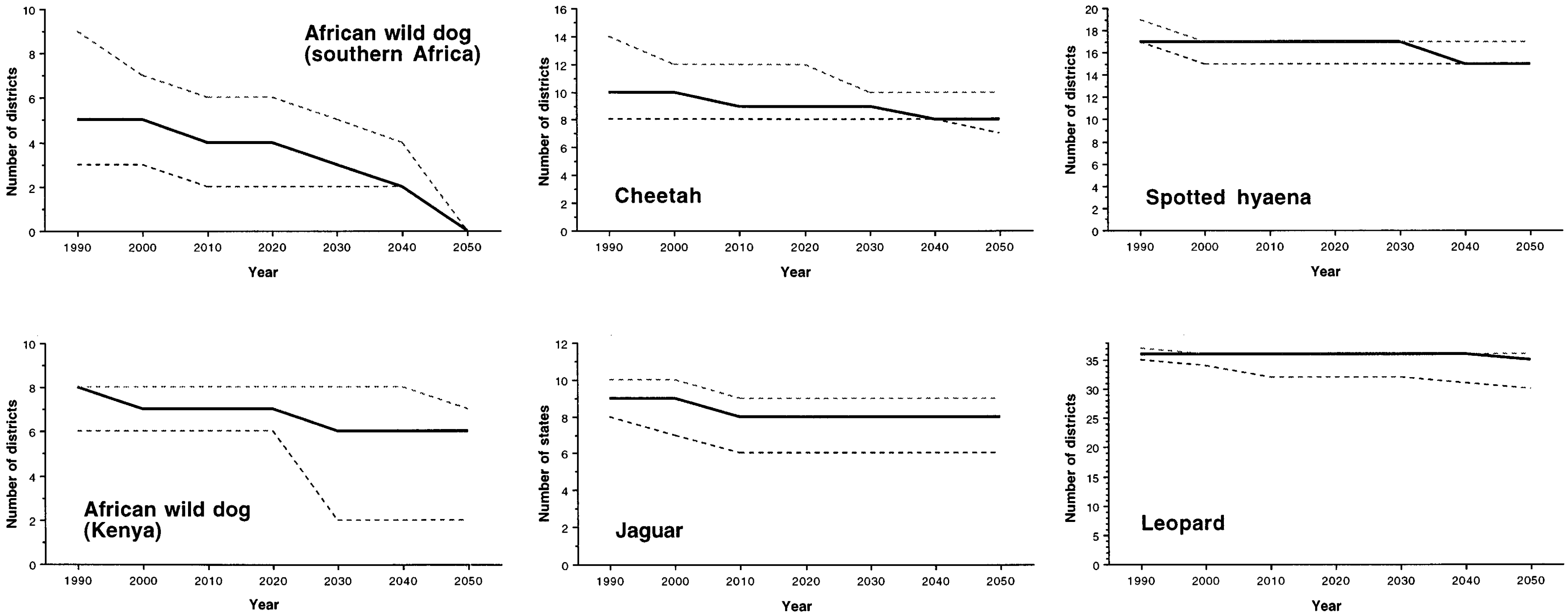

Fig. 3. Possible future carnivore declines, predicted by assuming that further extinctions will occur when local human density exceeds the critical levels presented in Table 1. Projected rates of national population growth are taken from U.S. Census Bureau (1999*a*); local density is assumed to change at national rates. Broken lines indicate margins of error, calculated using the upper and lower estimates of critical density. Note that, for reasons discussed in the text, these graphs are not expected to provide an accurate picture of future declines, and are presented for illustrative purposes only.

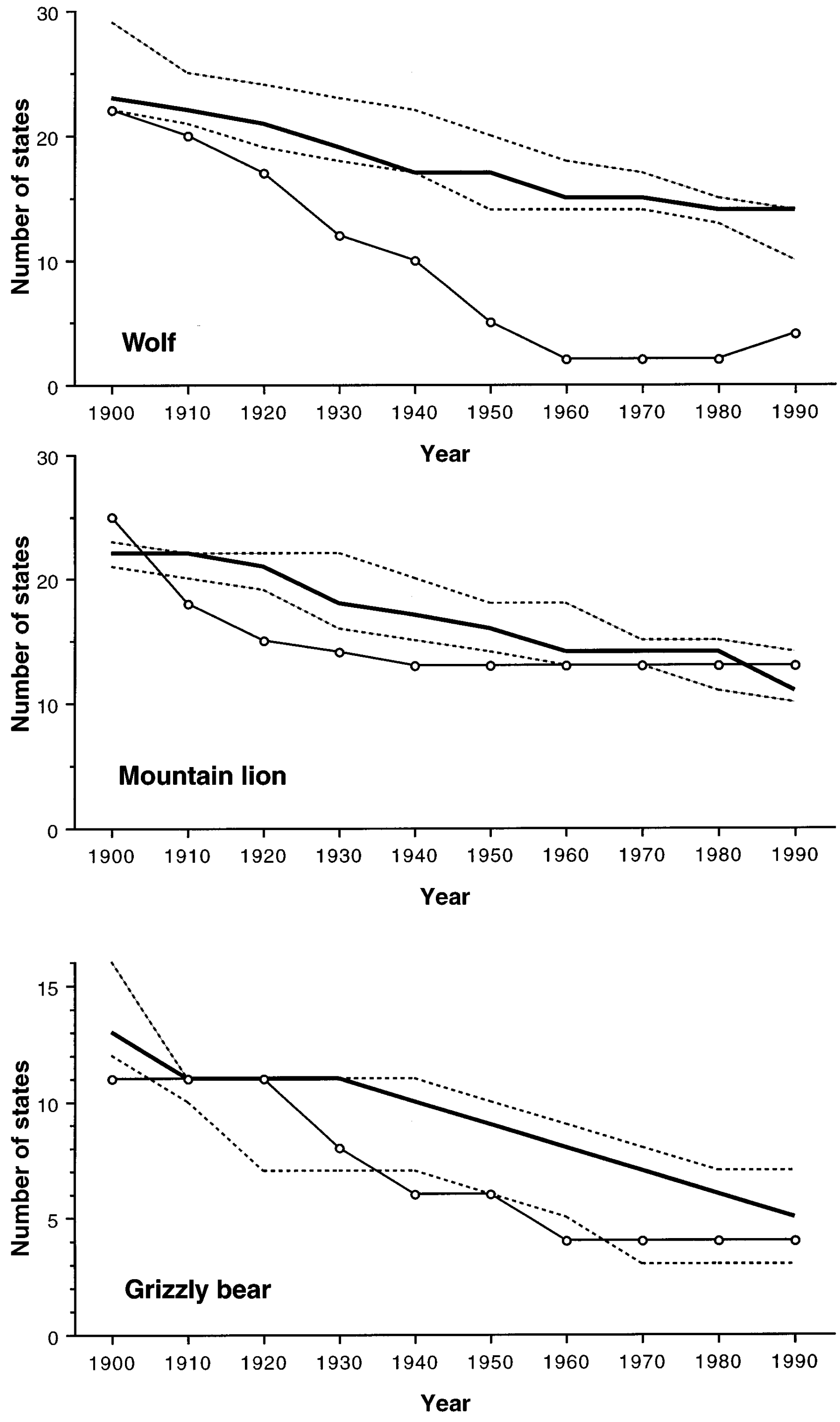

Fig. 4. Comparison of observed and expected rates of carnivore decline in the USA. Circles linked by continuous lines show the observed numbers of states still containing populations of wolves, mountain lions and grizzly bear during the period 1900–1990. Heavy continuous lines show the number of states predicted to hold populations, on the basis of estimated critical human densities and observed growth in local human populations. Broken lines give margins of error surrounding the predictions, based upon upper and lower estimates of critical human density. (Data sources: Young & Goldman, 1944; McCracken, 1957; Nowak, 1976; Peek *et al.*, 1987; Thiel & Ream, 1995; Nowell & Jackson, 1996; U.S. Census Bureau, 1999*b*).

kilometres; yet black bear populations are known to require much smaller areas to persist (Woodroffe & Ginsberg, 1998). In this case, the spatial scale used was more suited to lower-density, more wide-ranging species such as wild dogs and grizzly bears.

While there is a general association between high human density and carnivore extinction, estimates of critical human density vary substantially between species. For some species, such as grizzly bears and African wild dogs, critical human densities are very low

(Table 1; Figs. 2(a), (b) & (c)). Such species are likely to have become locally extinct as a direct result of human persecution, in habitats that had, thus far, been modified relatively little in other ways. Other species, such as leopards and spotted hyaenas, have much higher critical human densities (Table 1; Figs. 2(h) & (i)). These species appear better able to adapt to habitats modified by people (both may be sighted in some towns in East Africa). This adaptability might reflect their avoidance of people through nocturnal activity, and their ability to survive by scavenging when natural prey are depleted.

Limitations to the explanatory power of human density

Despite the associations described above, several lines of evidence suggest that human density alone may be a rather poor predictor of carnivore extinctions. First, carnivores' sensitivity to high human density appears to vary between regions as well as between species. Estimates of critical human density are substantially different for African wild dogs in eastern and southern Africa, and for cheetahs in Africa and India (Table 1, Figs. 2(a) & (c)). Further evidence of regional variation in carnivores' vulnerability comes from comparing the estimates of critical density presented in Table 1 with human densities in other regions where the species still persist. For example, the distribution of wolves in North America in 1900 suggested a critical human density of 13.0 people/km^2 (Table 1); yet, today, wolves persist in Cantabria, Spain (99 people/km^2), in Abruzzo, Italy (118 people/km^2), and in Rajasthan and Gujarat, India (129 and 211 people/km^2 respectively) where human densities are markedly higher (Delibes, 1990; Jhala & Giles, 1991; India Network Foundation, 1999; Instituto Nacional de Estad'stica, 1999; Istat, 1999). Clearly, 13 people/km^2 is not an upper limit for wolf persistence in all regions. Wolves' ability to survive in such populous areas may, once again, reflect their ability to adopt a nocturnal scavenging habit (Boitani, 1992).

The data presented in Fig. 4 suggest temporal as well as regional variation in human impact upon carnivores: in the course of the 20th century, large carnivores have declined more rapidly in the USA than would have been predicted from human population growth. This, too, suggests that some other factor, in addition to human density, contributed to predator declines.

Such regional and temporal variation might be caused by phenotypic variation among carnivores; however, it is much more likely to reflect both people's willingness to tolerate predators, and their ability to kill them. Several further examples suggest that local attitudes to predators strongly influence their chances of persistence. Cheetahs were tolerated or even prized in India until the arrival of British colonists, who not only hunted them, but introduced local noblemen to the sport (Divyabahnusinh, 1995). Indians' tolerance of carnivores was frowned upon by some of the colonists, as indicated by Burton's (1933) comment that, in the Punjab:

> *. . . tigers [are not] likely to be seen again until the withdrawal of British rule once more exposes the country to the anarchy and devastation which formerly oppressed it, leading to the extermination of populations, the reduction of agriculture, and the letting in of the jungle.*

Such cultural differences were also apparent in Africa: in 19th century Cape Province, lions persisted some 30 years longer in black homelands than in white-dominated areas, despite higher human densities (Skead, 1987).

Government policies may also influence peoples' tolerance for predators. Many goverments have, in the past, sponsored campaigns to eradicate species considered 'vermin', either by employing professional hunters or by paying bounties to people who could show evidence of having killed a predator. Such government-sponsored persecution probably explains why wolves and mountain lions declined more rapidly in the USA than predicted on the basis of rising human density (Fig. 4). Policies of this kind increase local 'demand' for dead predators and magnify human impacts upon carnivore populations.

Regional and international trade in carnivore skins, bones and other body parts may also encourage local people to kill predators. This might explain the recent increases in the killing of tigers (*Panthera tigris*) by Indian villagers who have, historically, co-existed with predators despite high human densities (Kumar & Wright, 1999). Likewise, local, regional or international trade that encourages depletion of carnivores' prey or destruction of their habitats will weaken relationships between local human densities and carnivore extinctions.

If local attitudes to predators play such an important role, then cultural, political and economic change will be as important as human population growth in determining carnivores' future. Fig. 3 predicts future carnivore declines solely on the basis of projected human population growth. Since human populations are expected to reach a plateau during the 21st century (U.S. Census Bureau, 1999*a*), the carnivore declines shown in Fig. 3 also level off for most species. However, since slowing of human population growth is expected to accompany economic development and cultural change, it may not result in a diminishing threat to predators. As economic demands rise, and agriculture becomes intensified, carnivore habitats will be modified, prey bases will be depleted, and people will, perhaps, become still less tolerant of predators.

Despite these concerns, political and cultural change may also permit the reversal of carnivore declines. The gradual recovery of wolves in the USA is testament to the possibilities: while the process is difficult and highly controversial, the fact remains that wolf numbers are increasing, despite continuing growth in human populations (Mech, 1995; Thiel & Ream, 1995; U.S. Census Bureau, 1999*b*). Likewise, the only species predicted (in Fig. 3) to become locally extinct by 2050 – the African wild dog in southern Africa – is currently experiencing population recovery in Zimbabwe, probably because of local changes in both land use practices and attitudes to predators (Rasmussen, 1997).

Such recoveries are encouraging, but it must be borne in mind that they represent recoveries – usually in areas of very low human density – from nationally-organized eradication campaigns. Under these circumstances, carnivores' status prior to recovery might not be expected to reflect either the density or tolerance of local people. Such recoveries may well be reversed as human activities intensify.

Using human densities to target future conservation efforts

Since cultural, political and economic effects appear to be so strong, are measures of human density of any value in planning future carnivore conservation efforts? Relationships with human density will be clearest – and predicted effects therefore most accurate – when the threat to carnivores comes directly from persecution or accidental killing by local people. Similar effects might be seen if harvesting of bushmeat for local consumption led to a depletion of prey bases. However, as discussed above, carnivore declines will be accelerated above the rate predicted from human population growth if, through political or economic forces, the factors driving the decline extend beyond the immediate locality. Nevertheless, since persecution and accidental killing by local people remain the most important causes of mortality for many predators (Woodroffe & Ginsberg, 1998), carnivore declines are likely to roughly track the expansion of human populations for some time to come.

In this context, projections of human population growth might be used to inform local efforts at carnivore conservation in the short term; population projections will be most accurate, and other factors most stable, under these circumstances. For example, analyses similar to those presented here might be used (1) to inform recommendations about the numbers of people permitted to inhabit buffer areas, (2) to assess the suitability of reintroduction sites, or (3) as part of the process of projecting future species' declines in implementing *Red list* criteria (IUCN, 1994). Further analyses, perhaps taking into account other measures of human activity (e.g. Ehrlich, 1994) might refine methods of predicting carnivores' future.

CONCLUSIONS

In conclusion, the data presented here indicate strong associations between local human density and carnivore extinctions. However, variation in local culture, government policy and international trade mean that human density alone is a poor predictor of carnivore extinctions. The importance of these factors may mean that extinction risks for carnivores will continue to increase, even as human population growth slows. This points to an urgent need for techniques to resolve conflicts between people and predators. The observations that, in some areas, people and predators co-exist even at high human densities, and that some carnivores have experienced population recoveries in both developed and developing countries, suggest that rising human densities may not inevitably lead to further carnivore extinctions if means can be found to promote co-existence.

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