Biodiversity and Conservation **10**: 1011–1026, 2001.

Human density as an influence on species/area relationships: double jeopardy for small African reserves?

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Received 21 December 1999; accepted in revised form 18 July 2000

Abstract. Small reserves are especially likely to lose species. Is that because the reserves are small, or because small reserves are located in especially adverse landscapes? It seems that the question has rarely, if ever, been asked. Data on reserve size and location in Africa, and calculations of local (within 50 km) mean human densities from available census records per province per country were the database here used to answer the question. IUCN grade I and II reserves in Africa are located across the range of human densities per country, including in regions of higher than average density. Furthermore reserve size correlates with local human density, such that small reserves are indeed significantly more likely than are large reserves to be located in regions of high human density ($n = 169$; $P < 0.0001$). However, while local human density correlates significantly with human-caused mortality of carnivores (the only taxon for which we had data), it does not correlate with detected extinctions in reserves in east Africa (the only region with available data). Rather, area of reserve is the main predictor. Nevertheless, abundant other evidence of the adverse effects of high human density on persistence of species and wilderness indicates that we need to take as a warning the findings reported here that small reserves occur in regions of high human density, and that human density correlates with human-caused mortality. They indicate that small reserves might face the double jeopardy of both their small size, and also their situation in especially hostile surroundings. In effect, small reserves are more isolated in more adverse habitat than current analyses in conservation biology, landscape ecology, or metapopulation analysis usually indicate.

Key words: Africa, edge effects, extinction, human density, protected areas, species/area relationships

Introduction

Small reserves (or habitat patches) are more likely to lose species than are large ones (Brown 1971; MacArthur 1972; Diamond 1975; Wilson et al. 1975; Wilcox 1980; Pimm 1991; Rosenzweig 1995; Laurance et al. 1997). Indeed, the relationship between size of a reserve, or habitat patch, and the number of species in the area is perceived as strong and consistent enough to be commonly used to predict times to extinction (Soulé et al. 1979; Belovsky 1987; Brooks et al. 1996, 1997), even though exceptions to the relationship exist (Turner 1996; Debinski et al. 2000). In addition, we know that the nature of the landscape around reserves also markedly affects processes operating within and between reserves, and hence affects the number of species in them (Lomolino et al. 1989; Naveh et al. 1994; Andrén 1995; Hansson et al. 1995; Hanski et al. 1997; Wiens 1997).

Abundant evidence indicates that one measure of nature of the landscape around reserves, human density, correlates with removal of natural habitat, damage to the environment, and extinction of species (Harcourt 1981, 1996; Parker et al. 1989; Barnes 1990; Hannah et al. 1994; Kerr et al. 1995; McNeely et al. 1995; Bawa et al. 1997; Hoare et al. 1999; Muchaal et al. 1999; Robinson et al. 1999). High human density is inimicable to conservation. Thus, common sense suggests that large reserves will be located and persist in areas of low human density, whereas small reserves will be most likely in regions of high human density (Hunter et al. 1993).

If human density correlates with extinction, and if small reserves are situated in regions of relatively high human density, then small reserves are in more adverse surroundings than are large reserves. They will suffer more intense edge effects, and will be more isolated. If so, some important external influences on species/area relationships might be missed if the relationship is analyzed as if the landscape around reserves was equally unsuitable around all reserves whatever their size, or as if the nature of the landscape matrix in which the reserves are located was random with respect to reserve size. If small reserves are more isolated or in a more adverse matrix than are large ones, the small ones are effectively smaller relative to the large than their gazetted size indicates (Newmark 1995). In brief, if size of reserve is associated with the nature of the matrix in which it is located, we must ask whether small reserves have few species because they are small, or rather, because they are situated in especially adverse landscapes, and are thus in effect both more isolated and more impacted than are large reserves. The two effects of reserve size on one hand and adverse landscape on the other are potentially different, with different implications for management.

Species differ in how they react to the same threat (Brown 1971; Terborgh 1974; Diamond 1984; Johns et al. 1987; Lomolino et al. 1989; Laurance 1990, 1991; Jablonski 1991; Leach et al. 1996; Harcourt 1998; Jernvall et al. 1998; Van Vuren 1998; Cowlishaw 1999; Harcourt and Schwartz 2001). Such differences are part of the reason why IUCN's criteria for listing the conservation status of species concentrate so much on biological characteristics of the species themselves, rather than on nature and intensity of the threats (IUCN 1996). If species react differently to different threats, the consequences for conservation management will differ greatly if local, external human influences have more of an impact on the integrity of a reserve than does reserve size itself, and process operating within the reserve. Of course, the two influences might interact, in which case the small reserves could suffer the double jeopardy of their small size and also their location in especially unfavorable surrounds.

As we have not been able to find any quantitative assessment of the relationship between size of reserves and nature of surrounding landscape, in this case, local human density, we therefore here ask for reserves in Africa whether reserves tend to be located in areas of low human density, whether the size of reserves correlates with local human density, and whether size of reserve or the local human density more strongly influences persistence of species in the reserve. We examine the relationship between reserve size and surrounding human density in Africa as a whole, and in individual countries in Africa.

Methods

Data on size, shape and site of IUCN category I, II and IV protected areas (reserves) in Africa, and on human density by administrative district, were taken from the Africa Data Sampler (ADS) CD (World Resources Institute 1995). The IUCN categorizes reserves according to management priorities; IUCN categories I, II and IV refer to strict nature reserves, national parks and managed nature reserve/wildlife sanctuaries, respectively. These categories are specifically for conservation of wildlife and involve exclusion of human use; other categories allow human use, or include cultural conservation.

The Sampler's population data is varied enough to find human density variations within countries and around different reserves within each country, as the ADS has a mean of 55 population polygons (administrative districts) per country in continental Africa. The ADS obtained it's data for human population from the National Center for Geographic Information and Analysis (NCGIA), and for the Protected Areas from the World Conservation Monitoring Centre (WCMC).

Our index of human density was the mean density in the 50 km wide zone around IUCN protected areas. In effect, a buffer 50 km wide was placed around each reserve, and the human density was calculated in these 50 km zones. This approach misses potential longer-distance effects, such as a major population center 75 km from the reserve. And of course, human density is merely an index of intensity of human use. The exact nature of the use is surely going to be important. However, a separate, far more detailed analysis is needed to account for such influences. The 50 km zone was delineated using the regions 'buffer' facility of ARC/INFO (ESRI Inc. 1998a). The human density was calculated in these 50 km zones using an Avenue script in ArcView, which calculated the total number of people in the 50 km zones, the total area of the 50 km zones, and divided the former by the latter for the mean human density in each 50 km zone. Even though the ADS has a mean of 55 population polygons per country, the ADS data is not detailed enough that it excludes human density from reserves (the population polygons overlap reserves; reserves do not have their own population polygons). Because of this lack of extremely fine detail, our mean human density in the 50 km zones may be slightly lower than actually exists (assuming that there are fewer people in a reserve than outside it). But also, we do not think that attempting to account for incorporation of the park area into the density estimates would be appropriate in the absence of exact information on, for instance, the number of people within reserves that were included in the censuses. Reserves on coasts (lake or sea) were given the 50 km zones only on the land.

Because of the sizes of some of the protected areas provided in the ADS CD data tables contrasted with sizes calculated from the coverages themselves, all sizes were calculated by using ArcView GIS (ESRI Inc. 1998b). IUCN category I and II contiguous protected areas were merged with ArcView GIS, so that values for reserve area and surrounding density for any 'reserve' is that for the single protected area formed by the contiguous reserves. Results and discussion involving IUCN category I, II and IV reserves (as opposed to simply IUCN grade I and II) have slightly different methods in the calculation of human density. In the analysis of IUCN category I, II and IV reserves, contiguous reserves were not merged and the 50 km zones included only the 50 km in the country within which the reserve was located (the 50 km zones do not overlap with other countries, which they did in the analysis of IUCN grad I and II reserves). Although this approach may be less applicable for biological reasons, we feel that is more applicable from a political, practical and economic standpoint on each country's placement of Reserves. The ADS is only a sampler. Missing countries are: Cape Verde, Comoros Islands, Djibouti, Guinea-Bissau, Libya, Sao Tome, Seychelles, and South Africa. Details for Kruger National Park, South Africa, were taken from Iremonger et al. (1997).

For comparing reserve area and human density as causes of extinction, we used Cox (1970). A model was fitted to the data:

P(reserve occupied) = [exp(A + B($\log_{10}$ reserve area) + C($\log_{10}$ human density))]/[1 + exp($A - B$($\log_{10}$ reserve area) + C($\log_{10}$ human density))] where A, B and C are constants.

Parameters were estimated by maximum likelihood to determine which significantly improved the fit of the model. The effects of reserve size and human density were assessed by dropping them from the model in turn, to estimate the contribution of each to total deviance. The resulting changes in deviance are distributed as ÷2 (df = 1). JMP (SAS Institute Inc. 1995) was used for statistical analysis unless otherwise stated. Statistical probabilities are two-tailed.

Results

Are reserves placed in empty regions?

We first ask whether reserves in African countries are usually situated in regions of relatively low human density. If they are, variation in human density around reserves is probably not an important influence on persistence of the reserves, or of species in them.

Most African reserves are not situated in regions of lower than average human density. Data are available on reserve size, surrounding human density, and country density for 33 countries in Africa (Table 1). The median ratio of the mean reserve's surrounding density per country to country's total density is 1.1, as if reserves are situated about randomly with respect to surrounding density. The value for the mean reserve's surrounding density could be biased upward by a high number of small reserves in areas of high human density. However, two other measures also indicate that reserves are sited across the range of human densities in Africa and its individual countries. These values are, per country, the median reserve's surrounding human density (reserves ranked by surrounding human density), and the human density for the reserve that falls at the 50% percentile of cumulative reserve area. These measures

Table 1. Mean density per km^2 of people in 50 km wide buffer around mean (area) IUCN grade I and II reserve in Africa compared to mean density of people per country (total human population/total area country) (see Methods for details of sources and calculations).

Country	Mean reserves density	Number reserves	Country density	Mean reserve density/ country density
Algeria	76	4	12	6.5
Angola	11	1	9	1.1
Benin	19	2	44	0.4
Botswana	2	5	2	0.7
Burkina Faso	40	3	37	1.1
Cameroon	43	7	29	1.5
Central African Rep.	3	5	5	0.6
Chad	10	3	5	2.1
Congo	2	1	7	0.3
Cote d'Ivoire	87	10	43	2.0
Ethiopia	55	10	47	1.2
Gabon	2	1	6	0.4
Gambia	85	2	88	1.0
Ghana	57	7	74	0.8
Guinea	27	3	26	1.0
Kenya	107	27	45	2.4
Liberia	11	1	30	0.4
Malawi	105	5	113	0.9
Mali	17	1	8	2.2
Morocco	110	1	41	2.7
Namibia	4	5	2	2.1
Niger	32	1	7	4.4
Nigeria	260	7	109	2.4
Rwanda	341	2	346	1.0
Senegal	15	3	41	0.4
Sudan	13	3	11	1.2
Tanzania	31	9	33	1.0
Togo	51	4	71	0.7
Tunisia	181	4	57	3.2
Uganda	113	5	88	1.3
Zaire (now D.R. Congo)	23	8	18	1.3
Zambia	12	18	12	1.0
Zimbabwe	20	11	29	0.7

give values for the median ratio of measure of reserve density to country density of 1.0 and 0.7, respectively. Thus, reserves in African countries seem not to be sited mostly in regions of low human density. The median country's human density around their mean, median, and cumulative 50% reserves is, respectively, 31, 27 and 14 people per km^2, compared to a median continent-wide density of 30 people per km^2. The higher two densities are up to twice the density at which, for example, elephant numbers appeared to crash in Zimbabwe (see also Parker et al. 1989; Hoare et al. 1999). The fact that a large number of reserves in Africa are in regions of high human density indicates that human density should be carefully examined as a potential influence on persistence of the reserves and species within them.

Does reserve size correlate with surrounding human density?

Given that a large proportion of African reserves are in regions of relatively high human density, and given that small reserves are already at risk merely because of their small size, it becomes important to discover if, as expected, small reserves are particularly likely to be in regions of high human density. The analysis is first done at the level of individual countries, because that is a common political unit for decisions concerning conservation. We then ask the question for the continent, because international conservation organisations are concerned with continent-wide relationships, even global relationships (e.g., Mittermeier et al. 1998).

Of the 33 countries for which we have the requisite data, 14 contain five or more IUCN grade I or II reserves, and 22 contain five or more IUCN grade I, II, or IV reserves. Eleven of the 14, and 19 of the 22 show a negative relation between size of reserve and surrounding human density; 3 of 11, and 7 of the 19 show a significant relationship; none shows a significant positive relationship (Table 2). At the continental scale, too, there exists a strong, significant, negative relationship between size of reserve (IUCN I and II), and surrounding human density ($P < 0.0001$; Figure 1). Thus, within African countries, and across Africa, small reserves are in regions of high human density, and large reserves in regions of low human density. This is not an unexpected result. The surprise is that it has been hitherto ignored, despite its crucial implications for predictions concerning extinctions in relation to size of reserves.

The establishment of a reserve can affect local human densities (Leader-Williams et al. 1990). Whether the small African reserves themselves caused the high local density (for some reason being more likely than large ones to attract to their borders a lot of people relative to the size of the reserve), or whether the high density caused the small size of reserves is immaterial at this stage. The point is that small reserves are in potentially more adverse surroundings than are large ones, and are thus in effect closer to their gazetted size than are the large ones, into and out of which species can more freely roam, and which suffer less intense edge effects (Newmark 1995).

Table 2. Countries with ≥five IUCN grade I, II, IV protected areas ($n = 22$), showing Spearman correlation coefficients, r_s, between area and surrounding human density, and significant probability values (i.e. $P < 0.1$) (Fisher combined probability test (Sokal et al. 1981): $\chi^2 = 61.5.0$, $P < 0.001$, df = 2, $n = 28$ for IUCN I and II; $\chi^2 = 83.0$, $P < 0.005$, df = 44 for IUCN, I, II, IV).

Country	Spearman r_s	n	P-value
Botswana	−0.05	8	–
Burkina Faso	−0.24	11	–
Cameroon	−0.87	10	0.002
Central Af. Rep.	−0.47	12	–
Chad	−0.93	6	0.03
Congo	0.43	6	–
Cote d'Ivoire	−0.71	12	0.02
Ethiopia	−0.58	18	0.03
Gabon	0.60	6	–
Ghana	−0.75	10	0.03
Kenya	−0.54	28	0.006
Malawi	−0.65	9	–
Mali	−0.50	5	–
Namibia	0.14	9	–
Nigeria	−0.11	13	–
Senegal	−0.90	6	0.03
Tanzania	−0.37	25	–
Togo	−0.43	11	–
Uganda	−0.36	19	–
Zaire	−0.63	8	–
Zambia	−0.24	18	–
Zimbabwe	−0.50	12	–

Is mortality or extinction related to reserve area or surrounding human density?

Given that some reserves in Africa occur in areas of high human density, and given that small reserves are especially likely to be in such areas, are reserves in areas of high human density more adversely affected than those in areas of low human density, once reserve size is taken into account?

First, does Africa match other regions in showing a relation between reserve size and number of species in reserves? Surprisingly few data exist to allow an answer to this question. While Soulé et al.'s (1979) seminal analysis indicated that large mammal species in east African Parks were more likely to go extinct in small reserves, the relationship was driven entirely by one abnormally small reserve, without which no relationship remains (r^2adj. $= -0.03$, $F_{1,16} = 0.5$, $P > 0.1$; see also (Western and Ssemekula 1981)). Part of the reason why the relationship might not be obvious in Africa is that for many of the species, suitable habitat still remains outside the gazetted reserves, and animals freely move across reserve boundaries (e.g. Harcourt 1996). In other words, because of low human density outside of reserves, reserve

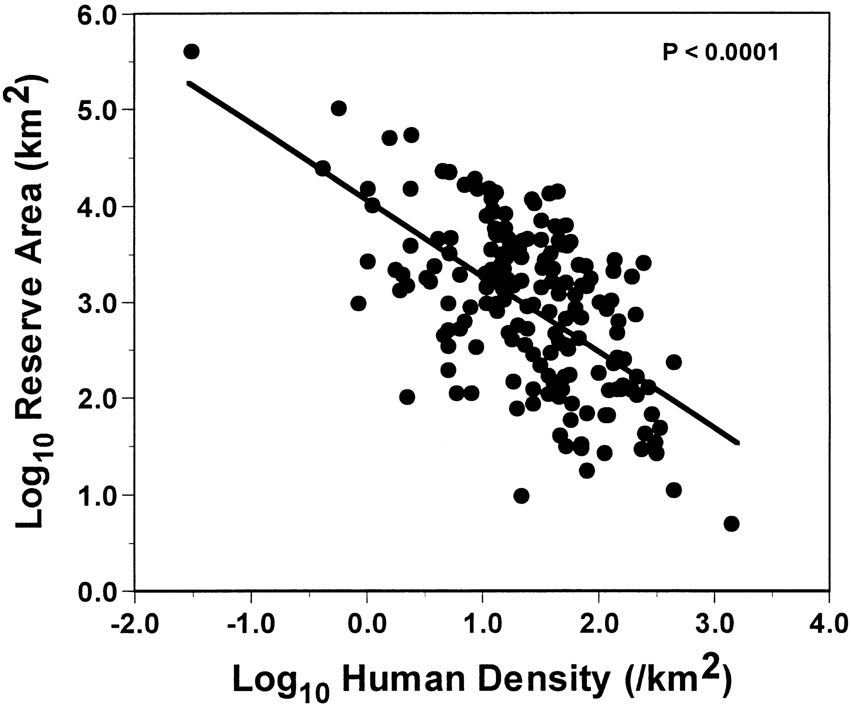

Figure 1. Log_{10} area (km^2) of IUCN category I and II reserves in relation to $\log_{10}$ local (within 50 km) human density (per km^2). Log_{10} area $= 4.0 - 0.75 \log_{10}$ density; r^2(adjusted) $= 0.32$; $F_{1,167} = 78.4, P < 0.0001$. Excluding six statistical outliers, $\log_{10}$ area $= 4.0 - 0.75 \log_{10}$ density; r^2(adjusted) $= 0.30$; $F_{1,161} = 70.6$, $P < 0.0001$). The relationship also holds when other subsets of the data are used, e.g. IUCN I, II and IV (r^2(adj.) $= 0.26$; $F_{1,284} = 101.9$, $P < 0.0001$).

area is effectively larger than the gazetted area (Newmark 1995). Nevertheless, Soulé et al.'s (1979) predictions of species loss in relation to area were later confirmed for ungulates in Tanzania's reserves (Newmark 1996; Burkey 1995), using species–area relationships of the Sunda Shelf islands, has predicted a faster rate of loss from east Africa's reserves than did Soulé et al. (1979). In addition, carnivores are significantly more likely to go extinct from small reserves than from large ones, especially those carnivore species that have a large home range, which takes them outside the reserve (Woodroffe et al. 1998).

Second, given that small reserves seem to be threatened, is mortality of species correlated with human density around the reserves? Data are available for carnivores in Africa. Woodroffe and Ginsberg's (1998) explanation for the fact that carnivore species with large home ranges were more susceptible (less able to survive in small reserves) than species with small home ranges was that species with large ranges were more likely to leave the reserves, and thus to be killed. Nevertheless, they did not investigate the influence of local human density. Data are available for reserve area, human density, and mortality caused by humans for eight protected areas in six

African countries across three carnivore species: wild dog *Lycaon pictus*, lion *Panthera leo*, and hyaena *Crocuta crocuta*. With respect to human density, these reserves are representative of Africa's reserves in total: human density around the reserves varied from close to zero to over 250 people per km^2 (with a median of 44/km^2), compared to country-wide densities of 2–45 with a median of 33 people per km^2: Four of the seven reserves were in regions with higher than average human density for their country (Table 3).

Because reserve area does not correlate significantly with surrounding human density for these particular reserves ($r_s = -0.48$, $n = 8$, $P > 0.3$), they provide a good opportunity to examine the independent effects of reserve area and surrounding human density. The comparison shows that human density, but not reserve area, correlates significantly with percent mortality by humans of the three species (Table 4; Figure 2). Woodroffe and Ginsberg (Woodroffe et al. 1998) argue that by comparison to harvesting and culling programs that have resulted in declines in carnivore numbers, the proportion of mortality caused by humans is so great (median of 42%, Table 3) that it could account for the carnivore extinctions detected within the species' former geographic range.

Third, given the correlation between human density and human-caused mortality, does extinction of species in reserves correlate with human density around reserves? It appears not. Size of reserve is a far better predictor of extinction in reserves of both ungulates in Tanzania, and of carnivores in East Africa than is local human density. The rate of ungulate extinctions in Tanzanian reserves correlates significantly with reserve area ($r_s = -0.93, n = 6, P < 0.02$) (Newmark 1996), but not with surrounding human density ($r_s = -0.32$, $P > 0.1$, this study). Neither value changes significantly if merged reserve area is used, nor with partial correlation analysis ($r_{\text{log density}}$ extinction rate $\times$ area $= -0.96$, $r_{\text{log area}}$ extinction rate $\times$ density $= -0.30$). Turning to

Table 3. Reserves in Africa for which data on area, surrounding human density and percent mortality of species caused by humans are available. Sources for area and density, and their mode of calculation in 'Methods'. The mortality data are from sources in Woodroffe et al. (1998).

Country	Species Reserve	Reserve area (km^2)	Reserve density	Country density	% Mortality by humans	Total mortality %
	Wild dog					
Zimbabwe	Hwange	14,876	9	29	81	–
S. Africa	Kruger	19,624	50	33	47	32
Botswana	Moremi	4048	0	2	7	26
Tanzania	Selous	43,690	18	33	25	–
	Lion					
Namibia	Etosha	22,045	5	2	25	5.5
Kenya	Nairobi	66	281	45	54	17
Tanzania	Serengeti	13,858	44	33	33	5.5
	Hyaena					
Kenya	Masai Mara	1725	84	45	61	–
Tanzania	Serengeti	13,858	44	33	42	7

Table 4. Statistics relating % mortality of carnivores caused by humans to reserve size and local human density (original data in Table 3). $*P < 0.05$, $**P < 0.01$.

Table 4a. Regression and Spearman correlation coefficient, r_s, results.

Linear regression	n	r^2 (adj.)	F	P-value	r_s	P-value
Log_{10} % mortality × $\log_{10}$ area[a]	9	−0.11	0.20	>0.1	−0.34	>0.1
Log_{10} % mortality × $\log_{10}$ human density[a]	9	0.45	7.49	<0.06	0.61	<0.08
Log_{10} % mortality × $\log_{10}$ area[a,b]	8	−0.08	0.45	>0.1	−0.53	>0.1
Log_{10} % mortality × $\log_{10}$ human density[a,b]	8	0.84	36.57	<0.01**	0.96	<0.01**
Residuals $\log_{10}$ % mortality × $\log_{10}$ human density against $\log_{10}$ area[a,b]	8	0.10	1.75	<0.1	0.46	>0.1
Residuals $\log_{10}$ % mortality × $\log_{10}$ area against $\log_{10}$ human density[a,b]	8	0.64	13.23	<0.03*	0.84	<0.01**
Log_{10} % mortality × $\log_{10}$ area[b,c]	7	−0.10	0.45	>0.1	−0.56	>0.1
Log_{10} % mortality × $\log_{10}$ human density[b,c]	7	0.84	32.02	<0.01**	0.96	<0.01**

[a] Serengeti counted twice, once for lions and once for hyaenas.
[b] The reserve Hwange is omitted because it is an outlier (see Methods). This is the regression and P value in Figure 2.
[c] Serengeti counted only once by averaging its lion and hyaena % mortality due to humans.

Table 4b. Partial correlation coefficients of $\log_{10}$ % mortality, $\log_{10}$ area and $\log_{10}$ human density.

Partial correlation coefficients	r
Log_{10} % mortality × $\log_{10}$ area[a]	−0.17
Log_{10} % mortality × $\log_{10}$ human density[a]	0.74
Log_{10} % mortality × $\log_{10}$ area[a,b]	−0.27
Log_{10} % mortality × $\log_{10}$ human density[a,b]	0.93
Log_{10} % mortality × $\log_{10}$ area[b,c]	−0.29
Log_{10} % mortality × $\log_{10}$ human density[b,c]	0.95

[a] Serengeti counted twice, once for lions and once for hyaenas.
[b] The reserve Hwange is omitted because it is an outlier (see Methods).
[c] Serengeti counted only once by averaging its lion and hyaena % mortality.

carnivores in East Africa, data on reserve area, surrounding density and presence–absence of the three carnivore species are available for 42 reserves in their former range in Kenya, Tanzania, and Uganda (Table 5). In this dataset, reserve area correlates inversely with surrounding human density ($r_s = -0.41$, $n = 52$, $P < 0.005$), unlike in the analysis of mortality rates. Logistic regression analysis (Cox 1970, see Methods) show that once area of reserve is accounted for, human density explains no more of the variation in extinction probability (Table 6). When $\log_{10}$ human density is used as the sole variable, none of the regressions are significant; all show significant effects when $\log_{10}$ reserve size is used as the sole independent variable (Woodroffe et al. 1998).

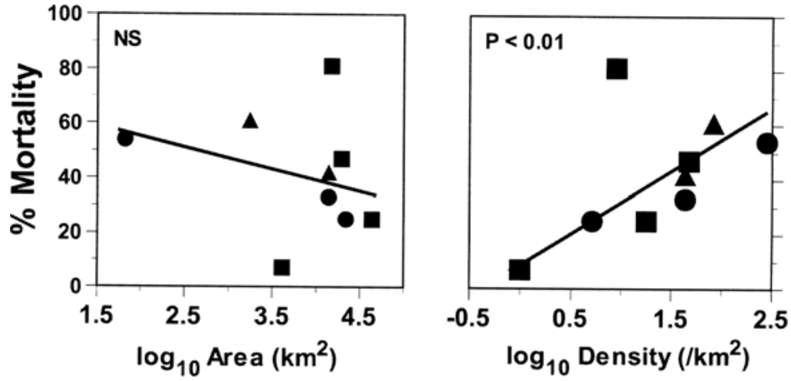

Figure 2. Percent mortality caused by humans of three species of carnivore (wild dog *Lycaon* (circle), lion *Panthera* (square)), and hyaena *Crocuta* (triangle) in eight protected areas in five countries in Africa (see Table 3). Statistical details in Table 4. The regression line is with the statistical outlier, Hwange, Zimbabwe, omitted (see Methods). The P value is also for Hwange omitted, and for the log–log data.

Discussion

By comparison to reserve area, local human density appears to be a negligible influence on persistence of species in east African reserves. This result does not allow complacency about outside threats to reserves, however. The extinctions discussed are those detected among carnivores (Woodroffe et al. 1998), and in large mammals in Tanzanian reserves (Newmark 1996), which were among only the antelopes. We know far too little about why taxa are differentially susceptible to extinction to explain why, in Tanzania, only antelopes should disappear, especially as carnivores have often been found to be particularly susceptible (Brown 1971; Diamond 1984; Heaney 1984). The effect needs to be tested on other taxa. The problem is that detecting extinction is extraordinarily difficult, in part because it requires proving a negative. Moreover, even if the data could be found, it seems likely that the lag between restriction of available habitat, and extinction is long enough for the effects of habitat restriction not yet to have become apparent (Soulé et al. 1979; Newmark 1995; Brooks et al. 1996; Brooks et al. 1997; Cowlishaw 1999). Whether an effect of human density on extinctions will be found in the rest of Africa remains to be seen. The prediction is that where human density is particularly high, effects of human density on extinctions will be seen.

If human density is found to correlate with probability of extinction within reserves, then given that small reserves are highly significantly likely to be situated in regions of relatively high human density, the small reserves will indeed be worse off than current analyses indicate. The current usual assumption in species/area analyses in conservation biology's models is that all reserves are in equally adverse surrounds. In effect the reserves have become islands in a homogeneous ocean of humanity. That is misleading. Misleading also is landscape ecology and metapopulation analysis that,

Table 5. Reserve area and surrounding human density of East Africa's 42 IUCN grade I, II and IV protected areas, plus estimated extinction of hunting dog, lion, and hyaena (blank = species not recorded before establishment of reserve; sources in Woodroffe and Ginsberg (1998)). Note that contiguous areas have been combined, and usually given the name of only one of the sectors.

Reserve name	Country	Area (km^2)	Human density/km^2	Wild dog	Lion	Hyaena
Aberdare	Kenya	721	205	No	Yes	Yes
Ajai	Uganda	177	73	No		
Amboseli	Kenya	402	34	No	No	Yes
Burigi	Tanzania	3186	75			Yes
Gombe	Tanzania	121	41	No	No	No
Hell's Gate	Kenya	119	141	No	No	No
Ibanda	Tanzania	248	123	No		
Katavi	Tanzania	1991	13	No	Yes	Yes
Katonga	Uganda	215	102	No		
Kibale Forest Corridor	Uganda	9166	104	No	Yes	Yes
Kidepo Valley	Uganda	1472	13	No	Yes	Yes
Kilimanjaro	Tanzania	1913	44	No	Yes	Yes
Kizigo	Tanzania	24,094	25	Yes	Yes	Yes
Kora	Kenya	1654	20	Yes	Yes	Yes
Lake Bogoria	Kenya	84	57	No		
Lake Manyara	Tanzania	559	20	No	Yes	Yes
Lake Mburo	Uganda	841	109	No	No	Yes
Lake Nakuru	Kenya	65	112	No	No	No
Marsabit	Kenya	1902	2		Yes	Yes
Matheniko	Uganda	5923	36	No	Yes	Yes
Meru	Kenya	853	66	No	Yes	Yes
Mikumi	Tanzania	47,146	18	Yes	Yes	Yes
Mkomazi	Tanzania	23,945	42	Yes	Yes	Yes
Mount Kenya	Kenya	610	146	No		Yes
Moyowosi	Tanzania	9506	36	Yes		Yes
Murchison Falls	Uganda	5124	49	No	Yes	Yes
Nairobi	Kenya	66	293	No	Yes	No
Nasolot	Kenya	76	19	No		
Ol Donyo Sabuk	Kenya	34	302	No		No
Rumanyika	Tanzania	390	96	No		
Saadani	Tanzania	94	42	No		
Samburu	Kenya	284	43	No	Yes	Yes
Serengeti	Tanzania	22,183	53	No	Yes	Yes
Shaba	Kenya	142	39	No	Yes	Yes
Shimba Hills	Kenya	225	125	No	No	No
Sibiloi	Kenya	1471	3		Yes	Yes
South Turkana	Kenya	1046	14	Yes		Yes
Tana River Primate	Kenya	111	6	No	No	Yes
Tarangire	Tanzania	4493	25	Yes	Yes	Yes
Toro	Uganda	507	62	No	No	No
Ugalla River	Tanzania	4843	15	Yes	Yes	Yes
Uwanda	Tanzania	5258	19		Yes	Yes

Table 6. Logistic regression results of extinction probability of three species of carnivore showing change in deviance (CID) due to dropping $\log_{10}$ reserve size and $\log_{10}$ human density as independent variables from the model (see Methods). $^*P < 0.05$.

CID due to	Species	n	CID	P-value
Log_{10} human density	*Lycaon*, wild dog	36	1.21	> 0.25
Log_{10} reserve size	*Lycaon*, wild dog	36	5.56	< 0.05*
Log_{10} human density	*Panthera*, lion	28	0.00	> 0.95
Log_{10} reserve size	*Panthera*, lion	28	5.73	< 0.05*
Log_{10} human density	*Crocuta*, hyaena	32	2.15	> 0.1
Log_{10} reserve size	*Crocuta*, hyaena	32	3.18	< 0.08

while it takes account of variation in the nature of the matrix around reserves, still takes no account of the connection between reserve size and the nature of the matrix. The results of this study indicate that small reserves might be in a more hostile matrix, a more hostile ocean, than are the large reserves.

Sensitive species will consequently find it more difficult to reach small reserves than is incorporated in current analyses. In other words, small reserves are either effectively smaller, or more isolated, than current analyses indicate. Emigrants from small reserves will be more likely to perish than will emigrants from large reserves. Thus, small reserves are even less likely to be rescued and even less likely to be a source of rescuers than current analyses indicate. Moreover, small reserves will suffer more intense edge effects than current analyses indicate: high local human density is likely to be associated with more incursions into the reserves by humans and their commensals. We know that a given edge intensity enters more deeply into small reserves than large. Now we must accept that the edge effect is not only going to go deeper, but start out more frequent or intense. In sum, time to extinction in small reserves could indeed be sooner than current analyses indicate (Soulé et al. 1979; Newmark 1995).

Practically, conservation organizations and governments have to make difficult decisions about where to put scarce resources (Leader-Williams et al. 1988; Ayres et al. 1991; Myers et al. 2000). One dichotomy can be between cheap use of resources in fairly safe sites, or expensive protection of especially threatened areas. If small reserves (or habitat patches) are surrounded by unusually high densities of people, the level of threat they face could be higher than the managers had hitherto considered, because the reserves face the potential double jeopardy of both their small size and also their especially adverse surroundings. In the present case, the analysis can be immediately used to pinpoint, for instance, reserves with especially high local densities for their size. Of the ten highest in sub-Saharan Africa (excluding southern Africa), four are in Nigeria, two in Rwanda, two of the more densely populated countries in Africa. Perhaps the most endangered IUCN I, II or IV reserve in Africa is Lekki Strict Nature Reserve in Nigeria: not only it is the smallest reserve in the dataset, but it has the highest local density for its size.

More theoretically, now that the correlation of reserve size and local human density has been demonstrated, and some adverse influence of local density has been demonstrated, the conservation oriented disciplines of conservation biology, landscape ecology and metapopulation analysis must surely take more account than hitherto of the double jeopardy faced by small reserves that results from their small size combined with their location in a more hostile matrix. That association between size and hostility of matrix can and should be incorporated into current models by decreasing the effective size of small reserves, and increasing the effective isolation of small reserves by comparison to large reserves.

Acknowledgements

We thank Pete Coppolillo, Susan Harrison, Nigel Leader-Williams, Kelly Stewart, Truman Young and an anonymous reviewer for comments that considerably improved the manuscript, and Sharon Collinge and Marcel Holyoak for discussion.

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