Reserve Size, Local Human Density, and Mammalian Extinctions in U.S. Protected Areas

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Abstract: *We examined quantitatively the interaction of reserve size and surrounding local human density in the United States and their relative effect on extinction of large mammals in 13 national parks of the western United States. Data on reserve size and human density were obtained from publicly available sources. Local human density was calculated as the mean density in the 50- or 100-km zone surrounding the reserves' borders. Reliable extinction data are extraordinarily hard to find. Using a variety of definitions of* extinct*, we collated information on extinctions of large mammals (>5 kg) that spanned the size of U.S. national parks as a whole. Human density surrounding reserves varies considerably. Overall, small reserves were in areas of higher human density than were large reserves (*$p < 0.0001$*,* $r^2 = -0.24$*,* $n = 864$*; excluding Hawaii), and many of the small reserves were at higher local density than the mean for the contiguous United States. Extinction rates of large mammals correlate significantly with local human density, but not with park area. These findings together emphasize that (1) processes occurring outside of a reserve's boundary may unexpectedly strongly affect species within the reserve; (2) small reserves might suffer the double jeopardy of not only their size but also their situation in especially adverse surrounds; and thus (3) small reserves might suffer more intense edge effects and be more isolated than large reserves. If so, conservation workers need to incorporate the relationship into their models and management decisions.*

Tamaño de Reserva, Densidad Humana Local y Extinción de Mamíferos en Áreas Protegidas de los Estados Unidos

Resumen: *Examinamos cuantitativamente la interacción entre el tamaño de la reserva y la densidad humana locales de sus alrededores en los Estados Unidos y sus efectos relativos en la extinción de mamíferos grandes en 13 parques nacionales del oeste del país. Los datos sobre el tamaño de la reserva y la densidad humana fueron obtenidos de fuentes públicas disponibles. La densidad humana local fue calculada como la densidad media en una zona de 50 ó 100 km de los alrededores de los límites de una reserva. Los datos confiables de extinción son extraordinariamente difíciles de conseguir. Usando una variedad de definiciones de la palabra* extinto *cotejamos la información sobre extinciones de mamíferos grandes (>5 kg) que abarcaban el tamaño de los parques nacionales de los Estados Unidos en su conjunto. La densidad humana circundante a las reservas varía considerablemente. En general, las reservas pequeñas se encontraban en áreas de mayor densidad humana comparadas con las reservas grandes (*$p < 0.0001$*,* $r^2 = -0.24$*,* $n = 864$ *[excluyendo Hawai]), y muchas de las reservas pequeñas tuvieron densidades locales más altas que la media de los Estados Unidos. Las tasas de extinción de mamíferos grandes se correlaciona significativamente con la densidad humana local, pero no con el área del parque. Estos resultados enfatizan de manera conjunta que (1) los procesos que ocurren fuera de los límites de una reserva pueden inesperadamente afectar de manera intensa a las especies de la reserva; (2) las reservas pequeñas podrían sufrir una amenaza doble no solo por su tamaño, sino también por su situación en ambientes circundantes especialmente adversos; (3) las reservas pequeñas podrían sufrir efectos de borde más intensos y ser más aisladas que las reservas grandes. Si es así, la conservación necesita incorporar esta relación en sus modelos y en la toma de decisiones para el manejo.*

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Introduction

A large literature on island biogeography and conservation biology suggests that small reserves, habitat islands, are more likely to lose species than are large ones, other things being equal. The usual explanations for the relationship concern processes operating within reserves. At the same time, a large literature on landscape ecology, including those parts of it associated with metapopulation analysis, examines the effects of use of the intervening matrix on the persistence of species in habitat patches. Nevertheless, the possibility that the size of reserves (or habitat patches) is itself linked to the nature of the local landscape has barely been considered, despite the common-sense perception that, for instance, large reserves or patches of natural habitat are unlikely to be situated or to persist in areas of intense human use.

Both the biology of extinction and the management implications of reserves are potentially very different if processes operating outside the reserve, rather than reserve size and internal processes, more strongly affect extinction (Rivard et al. 2000). Thus, it is crucial to investigate the relationship between reserve size and human impact in the region, and if there is a relationship, to distinguish the effects of reserve size from those of local human use.

Leader-Williams et al. (1990) suggest that national parks were frequently placed in areas unsuitable for intensive agriculture, such as upland areas of Britain, but they said nothing about the size of reserves in relation to human use. Hunter and Yonzon (1993) suggest that the large reserves at high elevation in Nepal could be so gazetted because of the low density of people there, but they did not quantitatively investigate the relationship. In fact, a large reserve at low elevation in Nepal results in no statistical relationship. But Harcourt et al. (2001) show that in Africa, a strong relationship exists on the continent as a whole, with small reserves in areas of high human density. We know of no other analyses of the relationship.

With respect to the relative strength of the influences of reserve area and local human use on extinction, Newmark (1996) argues that because he detected a strong influence of reserve size on extinction in Tanzania, local human use was effectively isolating the reserves. Similarly, Woodroffe and Ginsberg (1998) argue that because carnivores with large annual ranges disappeared from small reserves sooner than did those with small annual ranges, the larger carnivores were suffering when they left the reserves. That argument was substantiated by Harcourt et al.'s (2001) demonstration that local human density outside African reserves correlated better with the recorded mortality of carnivores than did reserve area. Lastly, in a detailed analysis of a variety of influences on diversity and extinction on Canadian reserves, Rivard et al. (2000) showed an adverse effect of local towns on extinction, with reserve size and regional productivity accounted for. They did not, however, specifically compare the relative influence of park area with that of outside use, in part because the effects were difficult to disentangle because a number of characteristics of the park (but not total park area) resembled those characteristics outside the parks.

If the relative influences of park area and local human use on extinctions are to be compared, a suitable measure of human use is needed. Rivard et al. (2000) used a variety of measures, but a single index would be particularly valuable. A large number of analyses show that high human density has strong adverse effects on the persistence of habitats and species (e.g., Kerr & Currie 1995; McNeely et al. 1995; Harcourt 1996; Woodroffe 2000). Human density is thus a logical first measure to use as an index of the intensity of human impact. Furthermore, abundant and precise databases of human density are available.

For North America, previous work suggests a strong influence of size of reserve on extinction. Newmark (1995) showed this for western North America, primarily the United States, and Gurd and Nudds (1999) and Rivard et al. (2000) showed it for Canada. Here we extended these studies by asking for the continental United States whether (1) reserve size correlates with surrounding human density, and whether (2) reserves are, on average, situated in regions of low human density. We then asked, for a subset of national parks for which we could obtain reliable information, whether (3) reserve size or local human density better predicts extinctions within the parks.

Methods

Data on Reserves

Data on the location and size of World Conservation Union (IUCN) grade I, II, and IV protected areas in the U.S. mainland were taken from Iremonger et al. (1997). These IUCN grades refer, respectively, to strict nature reserves, national parks, and managed nature reserves/wildlife sanctuaries—henceforth, reserves. Other grades of IUCN reserves were not analyzed because most were not established to protect biodiversity but to preserve landmarks or cultural artifacts, and in some instances allow for normal human activities. Most of the reserves in the source data were simply "relative area ellipsoids." Consequently, the shapes of the reserves were not available. Thus, contiguous reserves could not be merged, as they were in our analysis for Africa (Harcourt et al. 2001). The merging of reserves involves the removal of common boundaries where contiguous reserves are adjacent to each other, thus creating one reserve out of two or more adjacent reserves. It is better to merge contiguous reserves, because the total size of contiguous reserves is a better reflection of the area available to the conserved species than is the size of the individual reserves separated by only a political boundary on a map. Reserves classified as marine, estuarine, or underwater were removed from the analysis because they could not sensibly be considered as having surrounding human density. Reserves on islands and those containing the following words in their names were not included in the analysis, because all or part of the surroundings could not contain humans: key, bay, island, cape, gulf, cove, lagoon, and slough. In instances where reserves, such as Badlands National Park, completely encompassed another reserve of different designation (such as a wilderness area), we included the data for only the larger reserve to avoid double counting.

Data on Human Density

Human population data from each 1990 census tract were obtained from the Census CD + Maps CD-ROM of Cornelius et al. (1998). Data on the size, site, and shape of the 1990 census tracts were downloaded from the U.S. Census Bureau's web site (U.S. Census Bureau 2000). A census tract is a small geographic area in which the Census Bureau collects various data, including population data. Our measure of human density surrounding reserves in the United States was the mean density in a 50-km-wide zone around each reserve. We used the mean, not the median or mode, because we wanted the value to reflect regions of concentrated density, such as cities, on the assumption that these would have an effect out of proportion to the area they covered—an assumption subsequently confirmed by Rivard et al.'s (2000) analysis showing that, with other factors accounted for, towns and cities in the 100-km buffer around Canadian parks correlated most closely with extinctions within the parks. We examined a subset of 13 national parks in the western United States for extinctions. We used a 100-km zone in addition the 50-km zone to test for potential longer-distance effects of human density. In cases where the 50- and 100-km zones around national parks overlapped into Canada, human density came from the Gridded Population of the World dataset (Tobler et al. 1995). We used the regions "buffer" facility of Arc/Info (Environmental Systems Research Institute 1998*a*) to delineate the zones. We omitted portions of the zones that extended into areas without census information (large lakes, seas, and other waters). An "avenue" script was created in ArcView (Environmental Systems Research Institute 1998*b*) to calculate the mean human density in each zone.

National Parks

The total sample size of IUCN grade I, II, and IV reserves was 864 for the overall analysis of reserve size in relation to surrounding human density. We used a far smaller sample for the analysis of these two measures in relation to extinction because obtaining reliable data on extinction is extremely difficult. We thus analyzed only western national parks. We originally attempted to use the same national parks as did Newmark (1995) in his analysis of extinctions in North America in relation to park size, but accurate information from original sources on extinctions in Canadian national parks was difficult to find. These parks—Waterton Lakes National Park, Manning Provincial Park, and the Kootenay-Banff-Jasper-Yoho park complex—were therefore omitted. Grand Teton National Park was omitted because the expansion of the park in 1950 dramatically increased the habitat types and the number of species within the park and because it was difficult to locate information on mammals in the park. We added Mesa Verde National Park because adequate information on its mammals was easy to obtain. Data on the site and shape of the parks were downloaded from the U.S. National Park Service's geographic information system website (U.S. National Park Service 2000). We merged Sequoia and Kings Canyon National Parks because they are contiguous. Parks sizes were obtained from Iremonger et al. (1997).

Extinction

For measures of extinction rates in reserves in relation to reserve size and surrounding human density, we considered only mammals larger than 5 kg in the orders Carnivora and Artiodactyla (excluding the marine mammals of Olympic National Park). This threshold was chosen to improve the chances that recorded extinctions were real extinctions. Our assumption was that smaller mammals were more likely to be overlooked. Thus, they were both less likely to be recorded as originally present and, if originally present, more likely to be recorded subsequently as unseen and therefore extinct. In addition, large animals are more prone to extinction than small animals, especially due to human influence (Caughley & Gunn 1996), so it is particularly important to understand the factors affecting their persistence and how they operate.

Judging extinction is difficult in general (May et al. 1995) and especially in the case of national parks. The U.S. National Park Service is largely a recreation service, not a data-collection service (Sellars 1997), and it does not have a consistent record of extinctions. Therefore, we used a variety of criteria to determine whether a mammal was indeed extinct. We examined any reference to the mammals of the region or park that we could locate. Park biologists, historians, and other employees were contacted to discuss the past and present mammal compositions of each park. Where sources contradicted each other, the majority viewpoint was used. Many of the mammals whose extinctions we assessed are quite rare. Sightings were correspondingly rare, so we were often uncertain of either presence or absence. Because of this lack of certainty, we compiled two lists of extinctions for each park. The "conservative list" contained species we were positive had become extinct in the national park (although they might subsequently have been reintroduced). The "liberal list" contained all species in the conservative list plus species that seemed to have disappeared from the park but for which the information was too vague to be absolutely sure. Lack of information about particular species could be attributed to misidentification of species; unverified observations based on track castings, scat, or photographs; historical records and species lists incomplete due to insufficient funds. Both lists could underestimate extinction if recolonization occurred and the extinction before recolonization was missed. Finally, in both Newmark's (1995) study and ours, the mere presence of a species in a park does not necessarily mean the park can harbor that species entirely. Some species migrate out of parks or are transients. However, most information is in the form of presence-absence data, with no details about the nature of the presence. Presence therefore had to be counted as persistence even if in fact the park could not harbor the species year-round, which is often the case.

Below we describe in detail the process by which we decided whether a species was placed on the conservative or liberal extinction list. Our criteria differed from Newmark's (1995). For comparative purposes, we also provide the results for a third set of definitions (Newmark 1995, Table 1). Our criteria for the conservative list were as follows: (1) The species was definitely present when a park was established but is not now known by the U.S. National Park Service to be present. A dramatic decrease in range occurred, which previously included the park but no longer does. (2) Or, the species was originally present but had to be reintroduced in or near the park, or reintroduction efforts are in progress (on the assumption that, if the authorities are reintroducing a species, they think the species is extinct or about to go extinct for example, the wolf [*Canis lupus*] in Yellowstone National Park). Our criteria for the liberal list are as follows: (1) Species on the conservative list are included on this list. (2) The species' date of extinction was close to that of the park's establishment but is not known with certainty (i.e., the species was originally present in the area but could have disappeared before the park was established). (3) Or, sightings of the species occur on rare occasions (usually by unqualified visitors) but are not verified (see above). (4) Or, the National Park Service has no recent records and is uncertain of the status of the species. (5) Or, the literature states only "probably extinct." (6) Or, a species was introduced or reintroduction efforts are in progress, but the extinction date is not known with certainty (see above).

Species were excluded from the study for the following reasons: (1) Habitat in the region is different from the habitat of the park, and the species has specific habitat requirements that match the surrounding area but not the park. These species were probably not originally present (e.g., pronghorn [*Antilocapra Americana*] in Lassen region). (2) Species occurs in the region but is known to enter the park on rare occasions only, usually due to a lack of habitat for the species in the park (e.g., caribou [*Rangifer tarandus*] in the Glacier region). (3) Species does not occur in the region but has been recorded in the park. Such observations are presumably misidentifications (e.g., white-tailed deer [*Odocoileus virginianus*] in Crater Lake).

For the two lists of extinctions, we created two different extinction measures. The "percentage extinctions" is the number of extinct species divided by the total number of species available for extinction (total number of species in park when established). The "extinction rate" divides each percentage-of-extinctions value by the number of years since the park was established (age of the park). Thus, this measure is the percentage of the park's species lost per year.

Also, because the conservative extinction list may be too conservative and the liberal list may be too liberal, we took the mean of the two values for both measures of extinction. Thus, we had six extinction values in total, arising from two measures of extinction (proportion and rate) at three levels of certainty of data (conservative, liberal, and mean).

Results

Reserve Area in Relation to Surrounding Human Density

In the United States, a statistically significant negative relationship existed between size of reserve (IUCN I, II, and IV) and surrounding human density (Fig. 1). The relationship held when the extremes were excluded, namely the large reserves of Alaska that occur in regions of low human density and the extremely small reserves of 1 km^2 or less (Fig. 1). The relationship also held for national parks alone and for reserves excluding national parks. Although the variance explained was small in the contiguous United States, the slope was steep (> -0.30). In brief, small reserves occurred in regions of high human density.

Also, a proportion of the reserves were in regions of higher than average density for the contiguous United States as a whole. (We did not include Alaska in the analysis because it is so obviously unusual, with its huge reserves and low human population density). The mean human density of the contiguous states was 31.75 people/km^2. The mean and median local (50-km zone) human density of reserves in the contiguous United States

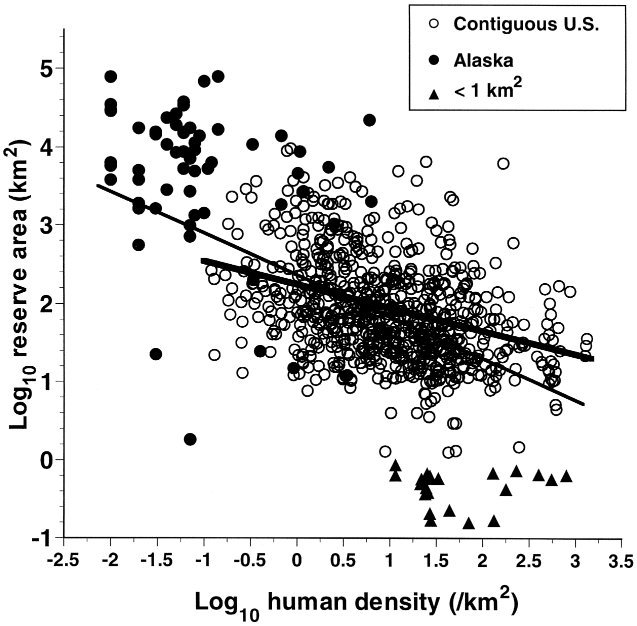

Figure 1. Results of least-squares regression for $\log_{10}$ reserve area against $\log_{10}$ human density (people/km^2) in 50-km zone around each reserve in the United States (IUCN categories I, II, IV), excluding Hawaii. Data for extremely small reserves and for Alaska are shown separately because Alaska has unusually large reserves and unusually low human density. For all comparisons, $p < 0.0001$. For $\log_{10}$ reserve area against $\log_{10}$ human density in 50-km zone [HD-50] surrounding reserve, r^2 adj. $= -0.24$, $n = 864$, slope $= -0.48$, $F = 280.5$; for $\log_{10}$ reserve excluding Alaska and reserves less than 1 km^2 area against HD-50, r^2 adj. $= -0.13$, $n = 796$, slope $= -0.30$, $F = 119.2$. The relationship holds only for national parks and for all reserves excluding national parks (contact authors for statistical details).

was 46.9 and 10.2 people/km^2, respectively. A quarter (25.2%) of the 823 reserves in the contiguous United States lie in regions with a higher human density than the mean for the contiguous United States. Human density surrounding reserves varies from as low as 0.12 to as high as 1333 people/km^2 in the contiguous United States. Such great variance, and the fact that a significant proportion of reserves are in regions of high human density, indicates that local human use should be examined carefully as a potential influence on persistence of the reserves and species within them.

Extinction in Relation to National Park Area and Surrounding Human Density

Several species appear to have gone extinct in national parks of the western United States (Table 1). In contrast to many other studies, including Newmark's (1995), probability of extinction did not correlate with park size in our sample (Table 2; Fig. 2a). Neither, convincingly, does original or current number of species in the park (original, $F_{1,12} = 6.83, p < 0.05$; Spearman $r_s = 0.62, p > 0.1$; current, $F_{1,12} = 5.85, p = 0.05$; $r_s = 0.56, p = 0.05$).

Based on either the liberal or the mean extinctions, however, probability of extinction correlated significantly with surrounding human density, whether extinction probability was measured as proportion of species extinct or as rate of extinction (i.e., proportion/duration of park's existence) (Table 2; Fig. 2b). In other words, a greater proportion of the original species present in the national parks have gone extinct and have become extinct at a greater rate in parks surrounded by relatively high human densities. Thus, over 45% of the variation in mean proportion of extinct species and in the mean extinction rate in the western national parks is explained by human density in the 50- or 100-km zones around national parks (Table 2).

Controlling for park size or human density, respectively, did not affect the independent associations: residual mean extinction rate $_{\text{log 50-km density}}$ against $\log_{10}$ park size ($r^2 = 0.01, p > 0.1$); residual mean extinction rate $_{\text{log park size}}$ against $\log_{10}$ 50-km density ($r^2 = 0.51, F = 11.7, p < 0.01$); partial correlation coefficients of mean extinction rate with $\log_{10}$ park size $= -0.08$ and with $\log_{10}$ 50-km human density $= 0.72$.

In sum, reserve area correlated negatively with local human density, indicating that small reserves are surrounded by a potentially more adverse environment than are large reserves. If there is a difference in the effects of reserve size and local human density on extinction, local human density appears to have more of an effect on extinctions than does reserve size: extinction rates of large mammals in national parks of the western United States correlated more strongly with local human density than they did with park size.

Discussion

Reserve Area and Human Density

Reserve size correlated with surrounding human density in the United States, as it does in Africa (Harcourt et al. 2001). Thus, in addition to the problems caused by the small size of the reserve itself, small reserves may suffer more intense edge effects than larger ones and may be more isolated. In effect, large reserves are safer than their gazetted size indicates. Analyses in conservation biology, landscape ecology, and metapopulation biology of the influence of reserve size on the persistence of reserves or the species in them probably need to take more account of this relationship between reserve size and local landscape, affecting as it does the effective size

Table 1. Data on national parks of the western United States used in analysis of park area and human density as determinants of species extinction.

National park (year gazetted)[a]	*HD-50*[b]	*HD-100*[c]	*Park area (km^2)*	*No. of species present at* T_0[d]	*Mean % extinct*[e]	*Mean extinction rate*[f]	*Conservative extinctions*[g,h]	*Liberal extinctions*[h,i]	*Newmark's (1995) extinctions*[h,j]	*Sources for extinctions*[k]
Bryce Canyon (1923)	0.57	1.29	144	8	0	0	none	none	red fox	1,2,3,4,5,6,7,8
Crater Lake (1902)	1.17	8.04	742	15	10	0.10	none	elk, lynx, wolverine	river otter	9,10,11,12,13
Glacier (1910)	3.88	2.85	4102	18	0	0	none	none	caribou	9,14,15,16,17,18,19
Grand Canyon (1906)	1.06	7.89	4934	12	8.3	0.11	wolf	wolf	raccoon	9,20,21,22,23,24,25
Lassen (1916)	2.87	9.65	433	11	4.5	0.05	none	fisher	fisher, river otter, pronghorn	9,26,27,28,29,30,31,32
Mesa Verde (1906)	5.64	4.00	208	12	12.5	0.13	wolf	wolf, bighorn sheep	did not analyze	8,9,33,34,35, 36
Mount Rainier (1899)	45.33	69.80	953	14	21.4	0.21	lynx	wolf, lynx, fisher, wolverine, elk	wolf, lynx, fisher	9,37,38,39,40,41
Olympic (1909)	23.47	92.92	3712	10	15	0.16	wolf	wolf, fisher	none	71,72,73,74,75,76
Rocky Mountain (1915)	30.76	50.87	1075	12	16.7	0.20	grizzly	grizzly, lynx, wolverine	none	9,42,43,44,45,47,48,49,77
Sequoia/Kings Canyon (1890)	15.89	19.71	3502	13	7.7	0.07	grizzly	grizzly	red fox, river otter	9,30,50,51,52,53,54
Yellowstone (1872)	0.92	2.70	8991	19	7.9	0.06	wolf	wolf, mountain lion	wolf[l]	55,56,57,9,58,59,60,61,62,63,64,71
Yosemite (1890)	4.73	24.93	3083	14	14.3	0.13	grizzly	bighorn sheep, grizzly, wolverine	none	9,30,53,65,66,67
Zion (1909)	4.21	1.82	593	10	10	0.11	bighorn sheep	bighorn sheep	raccoon	1,2,6,8,9,68,69,70

[a] *Year reserve was established. If originally a reserve of different designation than a national park, we used the earliest date of reserve establishment.*

[b] *Mean human density (HD) in 50-km zone surrounding park.*

[c] *Mean human density in 100 km surrounding park.*

[d] *Number of species present at time of park establishment; excludes species that immigrated or were introduced.*

[e] *Mean value of liberal and conservative percent extinctions (no. extinct species/no. species originally present).*

[f] *Mean extinction rate (mean % extinctions/reserve age).*

[g] *Extinctions that follow our "conservative" rules (see methods).*

[h] *Extinctions that follow our "liberal" rules (see methods).*

[i] *Species: bighorn sheep (*Ovis canadensis*), caribou (*Rangifer tarandus*), grizzly bear (*Ursus arctos*), elk (*Cervus elaphus*), fisher (*Martes pennanti*), lynx (*Lynx lynx*), mountain lion (*Felis concolor*), pronghorn (*Antilocapra americana*), raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), river otter (*Lutra canadensis*), gray wolf (*Canis lupus*), wolverine (*Gulo gulo*).*

[j] *Includes only species that we also analyzed for extinction.*

[k] *Sources available from authors.*

[l] *Newmark (1995) analyzed Grand Teton and Yellowstone National Park as a contiguous reserve.*

of the reserve, degree of isolation, and intensity of external influence on processes internal to the reserves. The association should be easy to incorporate into existing quantitative models.

We have implied throughout that human density determines where reserves are located: large reserves cannot be located in regions of high human density. Of course, the mere existence of a reserve, especially a national

Table 2. Results of analysis of extinction of large mammals in national parks of the western United States in relation to park area and local human density.

Extinction variable[a]	*HD zone*[b]	r^2 *adj.*[c]	F *ratio*[d]	$p \le$[e]	*Spearman* r_s[f]	$p \le$[e]
Conservative extinctions (%)	50	0.25	5.08	0.10	0.55	0.06
Conservative extinctions (%)	100	0.12	2.63	> 0.10	0.30	> 0.10
Liberal extinctions (%)	50	0.38	8.27	0.04*	0.64	0.02*
Liberal extinctions (%)	100	0.53	14.78	0.01**	0.68	0.01**
Mean extinctions (%)	50	0.47	11.84	0.02*	0.78	0.01**
Mean extinctions (%)	100	0.54	15.25	0.01**	0.71	0.01**
Conservative extinction rate	50	0.19	3.89	> 0.10	0.49	0.10
Conservative extinction rate	100	0.09	2.24	> 0.10	0.29	> 0.10
Liberal extinction rate	50	0.41	9.45	0.03*	0.66	0.02*
Liberal extinction rate	100	0.58	17.26	0.01**	0.76	0.01**
Mean extinction rate	50	0.46	11.42	0.02*	0.78	0.01**
Mean extinction rate	100	0.54	15.27	0.01**	0.70	0.01**
	log PA size[g]					
Conservative extinctions (%)	log size	−0.01	0.86	> 0.10	0.16	> 0.10
Liberal extinctions (%)	log size	−0.09	0.0013	> 0.10	−0.04	> 0.10
Mean extinctions (%)	log size	−0.09	0.044	> 0.10	−0.01	> 0.10
Conservative extinction rate	log size	−0.04	0.50	> 0.10	0.22	> 0.10
Liberal extinction rate	log size	−0.09	0.038	> 0.10	−0.09	> 0.10
Mean extinction rate	log size	−0.09	0.016	> 0.10	0.02	> 0.10

[a] *Extinctions refer to our two measures of extinction at three certainty levels for two human density zones surrounding the subset of national parks for which we measured extinctions. "Extinctions (%)" refers to percent of species extinct.*

[b] *Mean human density (people/km²) in 50- or 100-km zone around park.*

[c] *Least-squares regression result for column a by column b.*

[d] F *ratio for linear regression.*

[e] *p ≤0.05; **p ≤0.01.

[f] *Spearman correlation coefficient.*

[g] *The* $\log_{10}$ *area of reserve, for comparison of extinctions based on area rather than human density.*

park, can considerably alter local human density by attracting users. Thus, U.S. national parks have a higher local human density for their size than do other reserves in the United States (intercept of human density by reserve area on $\log_{10}$ human density of 2.56 for national parks, as opposed to 1.94 for the others in the sample). The same is true if creation of a reserve involved moving inhabitants of the region to the edges of the reserve (Newmark 1996). For the purposes of this preliminary analysis, the cause of the local density, high or low, is irrelevant (although some special arguments might be needed to demonstrate how small reserves would cause higher local densities than would large reserves). The fact is that whichever way the cause-effect relationship operates, small reserves are located in areas of higher density than large ones. Hence, the small reserves are located, other things being equal, in a more adverse landscape.

Extinctions

In contrast to previous results, we did not find an effect of park area on extinctions of large mammals in national parks of the western United States. Instead extinctions seem to be driven by local human density. In Canada, influences external to parks might be as severe as internal influences. The number of species "missing" and assumed extinct from Canadian national parks in Gurd and Nudds' (1999) sample correlates not just with park area, as they showed, but also significantly with local human density ($r^2 = 0.41$, $p < 0.05$: our analysis using Gurd and Nudd's data on extinctions). And in far more detail, Rivard et al. (2000) found effects of both park area and external human influence on extinctions, although they did not use human density as a measure. As far as we know, however, ours is the first demonstration of the greater influence of local human density than park area on extinctions.

Our findings differ from Newmark's (1995) analysis of extinctions in western parks, probably because our analyses differed. Newmark's sample of parks differs from ours, as do his definitions of extinction. Newmark (1995) tested several definitions of extinction, as we did. He assumed that a species was extinct if it had not been sighted for a minimum of 10 years, or 16 years, based on observation records from each park, whereas we had no minimum period. Also, we analyzed only species of over 5 kg—the most visible and most likely both to be seen and noticed as extinct—whereas Newmark (1995) included the Lagomorpha and all species of Carnivora and Artiodactyla independently of body mass. Even within our range of species, however, the identity of extinct species differed, presumably in part because of our dif-

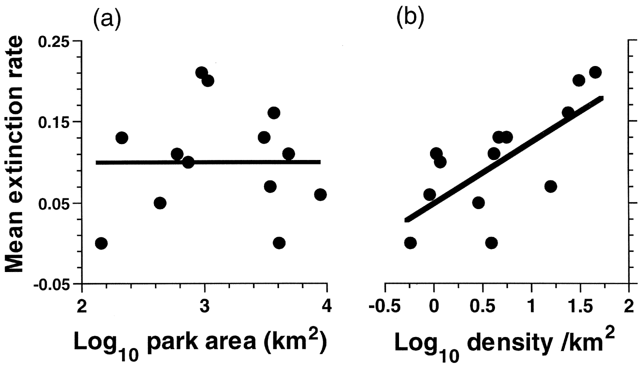

*Figure 2. (a) Mean extinction rate per national park of the western United States (*n = 13*) against* $\log_{10}$ *park area (km*^{2}*) (mean extinction rate ± 0.088 + 0.005* $\log_{10}$ *park area:* r^2 *adj. = −0.09;* $p > 0.1$*; Spearman* $r_s = 0.02$, $p > 0.1$*), and (b) mean extinction rate per national park of the western United States (*n = 13*) against* $\log_{10}$ *mean human density in 50-km zone (HD-50) around the park (mean extinction rate = 0.052 + 0.076* $\log_{10}$ *HD-50;* r^2 *adj. = 0.46;* $F_{1,12} = 11.42$*;* $p = 0.012$*; Spearman* $r_s = 0.78$, $p < 0.01$*).*

ferent definitions of extinction. Finally, Newmark (1995) included only natural extinctions. Several of the species deemed extinct by Newmark (1995) were also targets of control programs (Calahane 1939), suggesting that these extinctions may not have been natural. However, Newmark (1995) did not find any differences in extinction rate between controlled and uncontrolled species. Our records do not discriminate between natural extinction and human-influenced extinction, such as that of species targeted by predator-control programs. We emphasize that this is a list of differences between our studies, not an argument about whose definitions are better. We discovered in the course of our analysis that the Park Service keeps such poor records of the biology of its parks that no person's list is agreed upon by any other person, as far as we can tell. It seems that either biologists must wait to conduct analyses of extinctions in U.S. parks until the Park Service is voted sufficient funds by U.S. citizens to maintain a usable database or that we must use available records as best we can.

Given the finding that local human density correlates with extinctions in national parks of the western United States, the main issue that needs further analysis is that of how extinctions several decades ago correlate with human densities in 1990. Currently, we can only suggest a correlation between density now and density in the past. This disparity between timing of the measures of the cause and of the effects is not one of human density alone: it also bedevils analyses of the influence of reserve size on extinction. Although several researchers have found effects of reserve size on extinction, reserves are not islands in many countries (Newmark 1995; Newmark 1996; Gurd & Nudds 1999). Therefore, the gazetted size of reserves, which is the data available on their size, is often not the actual size of the area used by species. These will match only when reserves become so isolated by surrounding development that the only available habitat is in the reserve and individuals cannot move between reserves. Until such isolation occurs, what is the effective size of a reserve? For example, 11 species of large mammals were recorded in Soulé et al.'s (1979) smallest (0.2 km^2) reserve in east Africa, although it is possible that none of the large mammals stayed there for even a day (see also Woodroffe & Ginsberg 1998). The same disparity between gazetted reserve size and area of available land for species that use the reserve is true of our sample of national parks of the western United States, and of Newmark's (1995): several species range outside parks. An obvious explanation for the disparity we demonstrate between the influences of park area and human density is that high local densities of humans effectively isolate reserves. As land outside reserves becomes ever more altered, we will surely see more extinctions of species whose persistence depends on having more land available than is in the gazetted reserve (Newmark 1995; Woodroffe & Ginsberg 1998).

Conclusions

As Harcourt et al. (2001) argue, a correlation between reserve size and local human density, coupled with an adverse effect of local human density, means that species-area analyses might need to incorporate greater disparity in the area of available habitat, greater effective isolation of smaller reserves, and probably more intense edge effects in smaller reserves than the data indicate. The nature of the matrix surrounding reserves (and other habitat patches) is a crucial component in modern analyses, but the data for the United States and Africa indicate that a common missing factor might be the correlation between patch size and nature of the matrix (and the ramifications of that relationship). If so, the conservation-oriented disciplines of conservation biology, landscape ecology, and metapopulation analysis might need to account for these relationships. Conservation management too might benefit from the idea that small reserves might be in more adverse surroundings. For instance, small reserves, which could most benefit from corridors, occur in landscapes least suitable to gazetting and maintaining corridors.

Of course, local human density is not the only factor that varies around reserves (Rivard et al. 2000). Reserves differ considerably in the nature of surrounding land use, socioeconomic conditions, laws, and attitudes. Although the crude measurement of human density explains extinctions in reserves in western U.S. national parks, conservation management surely needs a more detailed understanding than it has of the processes by which surrounding land use and other factors affect the integrity and persistence of protected areas in relation to their size and the species in them.

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