

# Human demography and reserve size predict wildlife extinction in West Africa

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Species–area models have become the primary tool used to predict baseline extinction rates for species in isolated habitats, and have influenced conservation and land-use planning worldwide. In particular, these models have been used to predict extinction rates following the loss or fragmentation of natural habitats in the absence of direct human influence on species persistence. Thus, where direct human influences, such as hunting, put added pressure on species in remnant habitat patches, we should expect to observe extinction rates higher than those predicted by simple species–area models. Here, we show that extinction rates for 41 species of large mammals in six nature reserves in West Africa are 14–307 times higher than those predicted by models based on reserve size alone. Human population and reserve size accounted for 98% of the observed variation in extinction rates between reserves. Extinction occurred at higher rates than predicted by species–area models for carnivores, primates and ungulates, and at the highest rates overall near reserve borders. Our results indicate that, where the harvest of wildlife is common, conservation plans should focus on increasing the size of reserves and reducing the rate of hunting.

**Keywords:** edge effect; extinction; human population; mammals; reserve size; species–area relationship

## 1. INTRODUCTION

The species–area relationship and its value as a tool in conservation biology have been the subject of much debate (Simberloff & Abele 1976; Simberloff 1986, 1992; Boecklen 1997). Nevertheless, the repeated use of species–area models to plan reserves (MacKinnon 1997; Soulé & Terborgh 1999), estimate extinction rates (Pimm *et al.* 1995; Brooks *et al.* 1997) and identify conservation hotspots (Ceballos & Brown 1995) indicates that they have become a mainstay of conservation policy and practice (e.g. Rosenzweig 1995; Pimm & Raven 2000). Often, species–area models are used to predict the number of species that will be lost as a result of ‘natural’ demographic processes when isolated patches of habitat are reduced in size (Soulé *et al.* 1979; Pimm & Askins 1995; Brooks *et al.* 1997, 1999). This approach provides ‘best-case’ models based on habitat fragment size alone, after the effects of humans on species persistence in fragments have been excluded. Thus, habitats in which humans negatively affect the persistence of species, for example by hunting or by introducing exotic predators or competitors, should display rates of extinction higher than those predicted by these models (Richman *et al.* 1988; Newmark 1996). Most of the world’s biological diversity occurs in regions where habitat loss is accelerating, and many protected areas experience high rates of resource extraction (Whitmore & Sayer 1992; Wilcox 1980; Kramer *et al.* 1997; MacKinnon 1997; Robinson *et al.* 1999; Cincotta *et al.* 2000; Myers *et al.* 2000). Thus, we expect that many reserves in these regions will suffer higher rates of extinction than those predicted by models that consider only the effects of fragmentation on species persistence.

We compared the roles of human influences and area effects by using 28 years of census data to calculate

extinction rates for 41 species of large mammals in six Ghanaian reserves that experience high rates of human disturbance (figure 1 and appendix A). To quantify the effect of humans on species persistence, we first compared rates of wildlife extinction in Ghanaian reserves with those predicted on the basis of reserve size alone, as calculated using Soulé *et al.*’s (1979) model of ‘benign neglect’, and, second, tested whether human density around reserves was a useful predictor of wildlife extinction inside reserves. We also compared the extinction rates of carnivores, primates and ungulates, and tested whether mammals occurring near reserve borders were more vulnerable to extirpation than those occurring in the interior.

## 2. METHODS

### (a) *Wildlife counts*

Counts of large mammals were conducted approximately monthly by rangers of the Ghana Wildlife Division while on 10–15 km foot patrols around ranger posts within reserves. Species recorded on five or more patrols during the first 3 years after park establishment were counted as present in that area’s initial complement of species. Species initially present but not recorded at least once between 1995 and 1999 were judged to have become extinct locally. Thus, only species not detected from 52–1010 transect counts, depending on the number of ranger posts per reserve, conducted over 5 years, were deemed to be locally extirpated. In each case, all species found in a reserve at the end of the study period were among that reserve’s initial complement of species. Final assessments of species presence and extinction were corroborated against species accounts provided in 21 government reports and five publications (see appendix B). All the reserves that we studied occur in savannah habitat.

### (b) *Extinction models*

To calculate the observed extinction rates, we used extinction models that compared the number of species of large mammals

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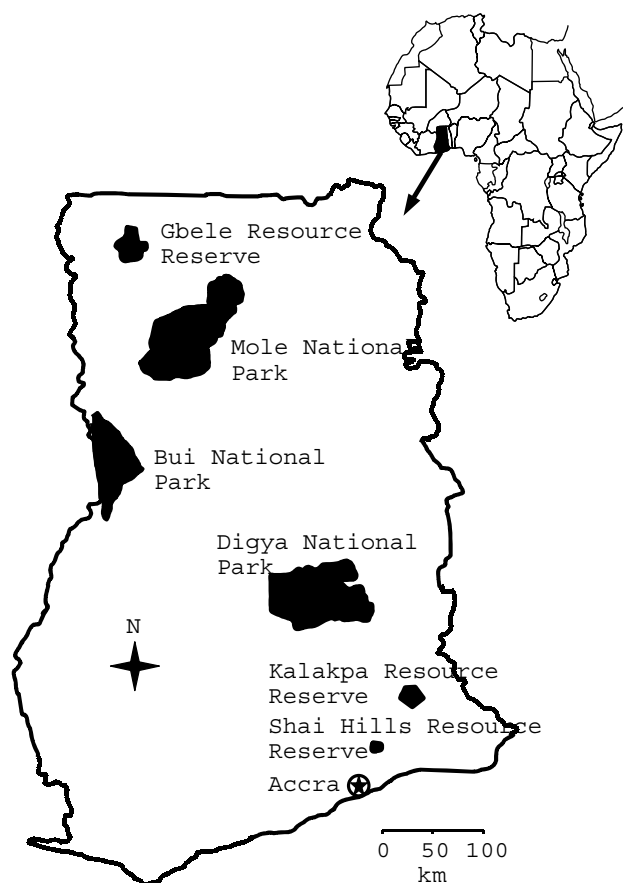


Figure 1. Locations of six protected areas in Ghana.

present at the time each reserve was created with the number present in 1998 (table 1). We used four extinction models,  $S^1$ – $S^4$ , based on the species–area relationship and evaluated in the literature (Diamond 1972; Soulé *et al.* 1979; Richman *et al.* 1988; Newmark 1996), to derive predicted and observed rates of local extinction. Each of these models is derived from the equation  $dS/dt = -k_n S^n$ , where  $k_n$  is the extinction parameter,  $n$  is an integer that defines the shape of the extinction curve,  $S$  is number of species and  $t$  is time since reserve creation (Soulé *et al.* 1979). We solved for the extinction parameter,  $k_n$ , following Richman *et al.* (1988). For example,  $k_2$  is given by

$$k_2 = \frac{(1/\text{historic species richness} - 1/\text{current richness})}{\text{time between initial and current}}. \quad (2.1)$$

Out of the models that we considered, the  $S^1$  and  $S^2$  models have predicted most accurately extinction rates for species in Africa and elsewhere (Richman *et al.* 1988; Newmark 1996). The results presented here are based on the  $S^2$  extinction model, but similar results were obtained with the  $S^1$ ,  $S^3$  and  $S^4$  models. One potential flaw of these models is that they predict the extinction of all species, given sufficient time; however, this is unlikely to affect the results of our analyses because of the relatively short time period considered in this study. Estimates of reserve area were taken from the literature (Sayer *et al.* 1992).

### (c) *Human demography*

We calculated the total human population within 50 km of each reserve by first identifying all human settlements with populations of over 100 people within 50 km of reserve borders on 1:500 000 scale maps, and then recording the population of each identified settlement using census data (Ghana Statistical

Service 1989; République de Côte d'Ivoire 1991). We used the human population within 50 km of each reserve to estimate human influence because hunters interviewed in Ghana indicated that large mammals harvested within reserves were seldom transported more than 50 km before being distributed or sold. Our results were similar when the human population within 25 km of each reserve was used in the regression models.

### 3. RESULTS AND DISCUSSION

We found that extinction rates in the six study reserves were 28 times higher, on average, than those predicted by models based on reserve size alone (figure 2*a*). Overall, reserves lost 21%–75% of large mammal species over a 27–30 year period, with no evidence of re-colonization. Although species became extinct at rates higher than those predicted by models based on reserve size, reserve size was closely correlated with extinction rate ( $r^2 = 0.86$ ,  $F_{1,4} = 24.5$ ,  $p = 0.008$ ).

As in much of West and Central Africa, wildlife is a common source of food in Ghana, and large mammals are hunted throughout the country and sold in local markets as 'bushmeat' (Asibey 1971, 1974; Manu 1987; Struhsaker & Oates 1995). Under the assumption that human population size was an estimator of demand for meat obtained by hunting, we explored whether hunting by humans could account for the high extinction rates in reserves, by tallying the size of the human population within 50 km of reserve borders (table 1), and then using this count as an independent variable in a regression of extinction rate on human population. We found a marked positive relationship between the size of the human population and the extinction rate ( $r^2 = 0.87$ ,  $F_{1,4} = 25.9$ ,  $p = 0.007$ ) (figure 2*b*). When reserve area and human population were included together in a regression model, nearly all of the variation in extinction rate between reserves was accounted for statistically ( $r^2 = 0.98$ ,  $F_{2,3} = 73.6$ ,  $p = 0.003$ ; partial correlation coefficients for extinction rate  $\times$  log area and extinction rate  $\times$  log human population size were  $r = -0.92$ ,  $p < 0.01$  and  $r = 0.93$ ,  $p < 0.01$ , respectively). However, the data were insufficient to separate definitively the correlated effects of human population size and reserve area on extinction rates (correlation coefficient of log human population size  $\times$  log area,  $r = -0.76$ ,  $p = 0.08$ ).

Woodroffe & Ginsberg (1998) speculated that human-induced mortality has resulted in high extinction rates for carnivores in reserves around the world. We found that extinction rates for carnivores were much higher than those predicted by species–area models (figure 2*c*). Extinction rates for primates and ungulates were also higher than those predicted by species–area models (figure 2*c*). Overall, reserve size was closely correlated with extinction rate in carnivores, primates and ungulates ( $r^2 = 0.86$ ,  $r^2 = 0.75$  and  $r^2 = 0.80$ , respectively;  $p = 0.02$  for all). The human population within 50 km of the reserve was also correlated with extinction rate in carnivores and ungulates ( $r^2 = 0.81$ ,  $p = 0.02$  and  $r^2 = 0.89$ ,  $p < 0.01$ , respectively). Field observations and market surveys suggest that primates are hunted heavily in Ghana; however, the human population within 50 km of the reserve was not correlated with extinction rate in primates ( $r^2 = 0.23$ ,  $p > 0.10$ ).

Table 1. Biogeographical and human population statistics of six protected areas in Ghana.

reserve	area (km <sup>2</sup> )	number of large mammal species			human population within 50 km
		1968–71	current	years of protection	
Mole National Park	4840	28	22	28	168 990
Digya National Park	3126	31	14	30	294 350
Bui National Park	2074	27	17	28	119 310
Gbele Resource Reserve	565	22	10	28	177 510
Kalakpa Resource Reserve	325	30	12	27	229 020
Shai Hills Resource Reserve	58	20	5	30	1383 710

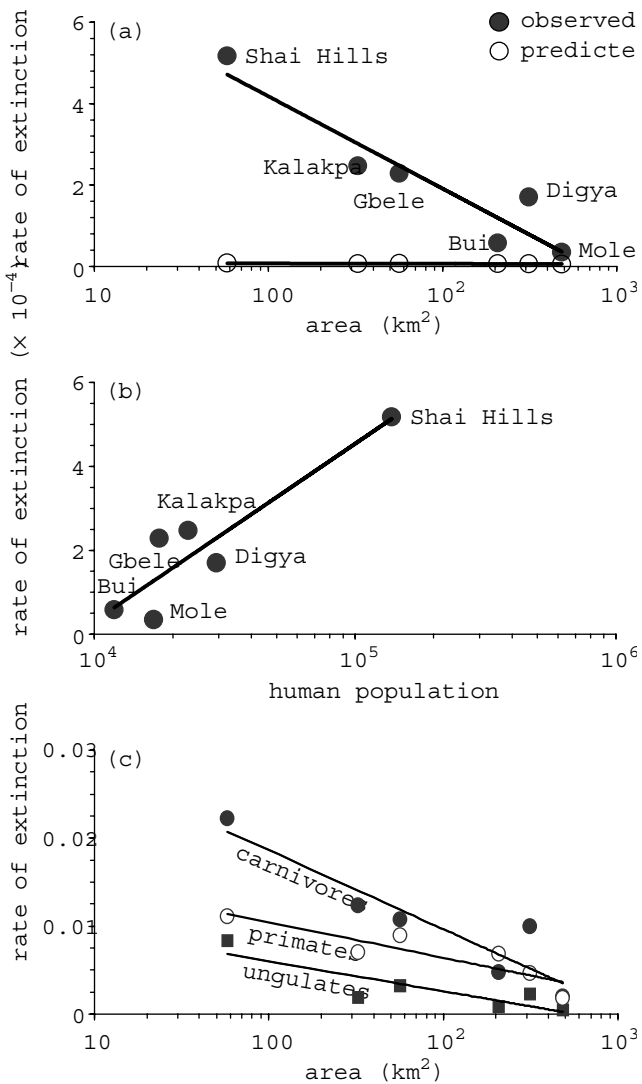


Figure 2. (a) Rate of local extinction of large mammals in Ghanaian reserves in relation to reserve area. Extinction rate is expressed in terms of the extinction coefficient,  $k_2$ . Observed extinction rates were, on average, 28 times higher than those predicted by the  $S^2$  extinction model. The upper line shows the relationship  $y = -0.001 \times \log(x) + 0.0087$  for the observed data. The predicted rates of extinction were calculated as  $y = -4 \times 10^{-6} \times \log(x) + 9 \times 10^{-5}$ , following Newmark (1996), and range from  $7.4 \times 10^{-5}$  for Shai Hills Resource Reserve to  $5.7 \times 10^{-3}$  for Mole National Park. (b) Rate of local extinction,  $k_2$ , of large mammals in Ghanaian reserves in relation to the total human population within 50 km of the reserve. (c) Rate of local extinction,  $k_2$ , of carnivores, primates

Our results are also consistent with the notion that hunting is most severe along reserve edges, and that the width of this edge-effect zone is influenced by the size of the local human population (Soulé 1986; Terborgh & Van Schaik 1997). We calculated site-specific extirpation rates using census data for 28 species of large mammals at 23 transect locations in Ghana's largest reserve, Mole National Park. To do this, we identified the precise locations of mammal counts within the reserve, and compared the number of species observed on counts between 1970 and 1973 with the number of species counted along the same census routes between 1995 and 1998. We found that the proximity of census routes to the boundary of the reserve was positively related to the rate at which species disappeared from the census routes ( $r^2 = 0.63$ ,  $F_{1,21} = 36.2$ ,  $p < 0.001$ ; figure 3). The proximity of census routes to the reserve boundary was also positively related to rates of local extirpation for carnivores ( $r^2 = 0.29$ ,  $F_{1,18} = 5.7$ ,  $p = 0.03$ ), ungulates ( $r^2 = 0.50$ ,  $F_{1,21} = 21.2$ ,  $p < 0.001$ ) and primates ( $r^2 = 0.37$ ,  $F_{1,17} = 10.2$ ,  $p = 0.005$ ) separately. These results are unlikely to have been caused by animals moving to the centre of the park over time, because the rates at which mammals disappeared were also 5.5 times higher than predicted by a species-area model for routes located in the inner 50% of the reserve (mean  $\pm$  s.e.m. at interior posts =  $3.18 \times 10^{-4} \pm 7.39 \times 10^{-5}$ ,  $n = 7$ ). Thus, species disappeared at accelerated rates over the entire reserve, but at the highest rates near its periphery.

Overall, our results suggest that humans have greatly influenced the persistence of large mammals in reserves in Ghana. Although the assertion that humans cause wildlife extinction is generally accepted, few studies have successfully identified quantitative links between the size of the local human population and species extinction (see also Campbell & Hofer 1995). Our results have several implications for conservation planning in areas of the world where the harvest of wildlife is common. First, the threat to biological diversity in West Africa is high relative to other countries in sub-Saharan Africa, and this has been attributed to high human population density and

and ungulates in Ghanaian reserves in relation to reserve area ( $n =$  seven carnivores,  $n = 10$  primates and  $n = 23$  ungulates). Extinction rates of carnivores in the six reserves were 36–300 times higher than those predicted by the  $S^2$  extinction model. Extinction rates of primates and ungulates were, respectively, 31–150 and 9–112 times higher than predicted.

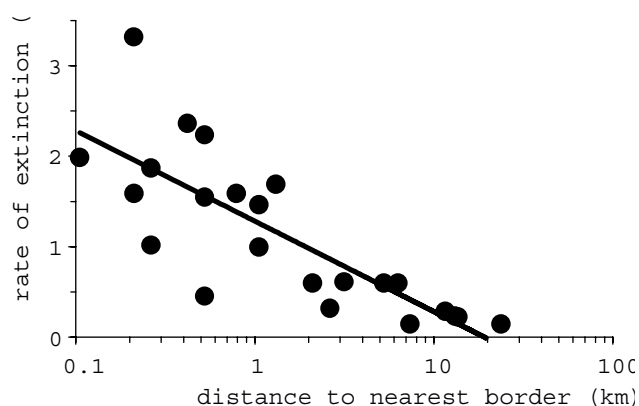


Figure 3. Rate of extinction of large mammals along census routes in Mole National Park in relation to the distance of the routes from the nearest park border ( $r^2 = 0.63$ ,  $F_{1,21} = 36.2$ ,  $p < 0.001$ ).

habitat loss (Sayer *et al.* 1992; Struhsaker & Oates 1995; Van Schaik *et al.* 1997; Oates 1999; Terborgh 1999). The human population in the developing world continues to grow rapidly (Urban & Nightingale 1993), suggesting that human pressure on reserves will increase. Thus, Ghana may provide a glimpse of the future for large mammals in reserves elsewhere if world conservation efforts are not intensified.

Second, extrapolation from the species-area model has led many researchers to suggest that conservation efforts should focus on creating habitat corridors between existing reserves (Newmark 1987, 1996; Saunders & Hobbs 1991; Wilcox 1980; Brandon 1997; Soulé & Terborgh 1999). Where reserve area is the dominant factor affecting species persistence, corridors may increase the amount of habitat available to wildlife, facilitate dispersal and gene flow, and reduce extinction. However, where hunting or other human influences accelerate extinction rates in reserves, animals that use corridors may simply become more vulnerable to hunting or other deleterious human influences (Simberloff *et al.* 1992; Woodroffe & Ginsberg 1998). Thus, where deleterious human influences severely affect wildlife, resources currently allocated to the creation of corridors might be spent more effectively in expanding the size of reserves, increasing the ratio of reserve area to edge and curtailing harvest.

Third, protected areas are a cornerstone of modern conservation planning, and envisioned as strongholds against the erosion of biological diversity (Brandon 1997; Bruner *et al.* 2001). Reserves in Ghana serve as refuges for many species that once occurred throughout the country, and wildlife habitat within these reserves remains intact. However, our results indicate that the reserves in Ghana are too small and hunting levels are too high for these areas to maintain populations of these species, and other reports suggest similar trends in reserves elsewhere in Africa, South and Central America, and Asia (Whitmore & Sayer 1992; Kramer *et al.* 1997; Van Schaik *et al.* 1997; Robinson *et al.* 1999; Terborgh 1999). This indicates that increased conservation planning and investment are required if protected areas in many parts of the world are to achieve their assumed role.

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#### APPENDIX A. MAMMAL SPECIES CONSIDERED IN THIS STUDY AND THEIR HISTORIC AND PRESENT-DAY REPRESENTATION IN SIX SAVANNAH RESERVES IN GHANA

species	common name	number of reserves in	
		1971	1998
<i>Syncerus caffer</i>	African buffalo	4	4
<i>Tragelaphus euryceros</i>	bongo	3	0
<i>Tragelaphus scriptus</i>	bushbuck	6	5
<i>Neotragus pygmaeus</i>	royal antelope	2	0
<i>Ourebia ourebi</i>	oribi	6	4
<i>Hippotragus equinus</i>	roan antelope	5	3
<i>Alcelaphus buselaphus</i>	hartebeest	6	4
<i>Sylvicapra grimmia</i>	bush duiker	6	4
<i>Cephalophus maxwelli</i>	Maxwell's duiker	2	1
<i>Cephalophus rufilatus</i>	red-flanked duiker	6	4
<i>Cephalophus dorsalis</i>	bay duiker	2	0
<i>Cephalophus ogilbyi</i>	Ogilby's duiker	2	0
<i>Cephalophus silvicultor</i>	yellow-backed duiker	4	0
<i>Cephalophus niger</i>	black duiker	2	0
<i>Kobus ellipsiprymnus</i>	waterbuck	6	4
<i>Kobus kob</i>	kob	6	5
<i>Redunca redunca</i>	reedbuck	5	2
<i>Hippopotamus amphibius</i>	hippopotamus	4	2
<i>Phacochoerus africanus</i>	warthog	6	4
<i>Potamochoerus porcus</i>	red-river hog	2	1
<i>Hylochoerus meinertzhageni</i>	giant hog	2	0
<i>Canis adustus</i>	side-striped jackal	2	1
<i>Lycan pictus</i>	wild dog	3	0
<i>Civetticus civetta</i>	African civet	2	1
<i>Crocuta crocuta</i>	hyena	5	1
<i>Panthera leo</i>	lion	5	1
<i>Panthera pardus</i>	leopard	5	3
<i>Felis aurata</i>	golden cat	2	0
<i>Felis serval</i>	serval cat	4	1
<i>Smutsia gigantea</i>	giant pangolin	3	1
<i>Loxodonta africana</i>	African elephant	3	1
<i>Orycteropus afer</i>	aardvark	2	1
<i>Colobus vellerosus</i>	black and white colobus	4	2
<i>Procolobus verus</i>	olive colobus	2	0
<i>Colobus badius</i>	red colobus	1	0
<i>Cercopithecus nictitans</i>	spot-nose monkey	4	2
<i>Cercopithecus mona</i>	mona monkey	4	2
<i>Cercopithecus patas</i>	patas monkey	5	4
<i>Cercopithecus aethiops</i>	green monkey	6	5
<i>Papio anubis</i>	anubis baboon	6	6
<i>Perodicticus potto</i>	potto	3	1

## APPENDIX B. REPORTS AND PUBLICATIONS USED TO CORROBORATE ASSESSMENTS OF SPECIES PRESENCE OR ABSENCE

### (a) Unpublished reports

Aberdeen University 1974 Aberdeen University expedition report no. 1.

Aberdeen University 1975 Aberdeen University expedition report no. 2.

Aberdeen University 1976 Aberdeen University expedition report no. 3.

Aberdeen University 1977 Aberdeen University expedition report no. 4.

Aberdeen University 1978 Aberdeen University expedition report no. 5.

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Ofori, B. Y. & Mensah, A. Y. 1971 A faunal survey of the Banda Watershed and the Lanka Forest Reserve. Accra: Department of Game and Wildlife.

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### (b) Publications

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