
Insularization of Tanzanian Parks and the Local Extinction of Large Mammals

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Abstract: *Island biogeography theory predicts that species will be lost on habitat "islands" created by the fragmentation of continental regions. Many Tanzanian parks are rapidly becoming habitat islands as a result of human settlement, agricultural development, and the active elimination of wildlife on adjacent lands. The rate of extinction of mammals in six Tanzanian parks over the last 35-83 years is significantly and inversely related to park area, suggesting that increasing insularization of the parks has been an important contributory factor in large mammal extinctions. I compared observed patterns of persistence of mammals in Tanzanian parks to predictions derived from earlier extinction models. The predictions of the S¹ models of Soulé et al. (1979) and Burkey (1994) and the S² and S³ models of Soulé et al. (1979) match very closely the observed pattern of persistence of mammals in Tanzanian parks. The loss of mammal species will probably continue, particularly in the smaller parks. Establishment of wildlife corridors linking the parks in northern Tanzania could help to reduce the potential loss of species in the future.*

Aislamiento de Parques de Tanzania y la Extinción local de mamíferos grandes

Resumen: *La teoría de la biogeografía de islas predice que se perderán especies en "islas" creadas por la fragmentación de regiones continentales. Varios parques de Tanzania se están convirtiendo rápidamente en hábitats "islas" como resultado de asentamientos humanos, desarrollo agrícola y al activa eliminación de vida silvestre en tierras adyacentes. La tasa de extinción de mamíferos de en seis parques de Tanzania durante los últimos 35-83 años es significativa e inversamente se relaciona con el área del parque, sugiriendo que el creciente aislamiento de los parques ha sido un factor que contribuye a la extinción de mamíferos grandes. Patrones observados de persistencia de mamíferos en parques de Tanzania son comparados con predicciones derivadas de modelos de extinción elaborados tiempo atrás. Las predicciones de los modelos S¹ de Soulé et al. (1979) se aproximan a los patrones observados de persistencia de mamíferos en los parques de Tanzania. La Pérdida de especies de mamíferos probablemente continuará, particularmente en los parques pequeños. El establecimiento de corredores que interconecten los parques del Norte de Tanzania podrían ayudar a reducir la pérdida potencial de especies en el futuro.*

Introduction

Island biogeography theory (MacArthur & Wilson 1967) proposes that the number of species in an isolated habitat is determined by the interaction of species colonization and extinction. This theory suggests that the rate of

species colonization is influenced primarily by the distance of an island from a colonizing source, whereas the rate of species extinction is determined primarily by population size, which in turn is influenced by island area.

One prediction of island biogeography theory is that habitat "islands" created by the fragmentation of continental regions should experience rates of extinction inversely proportional to their size. Empirical support of this prediction is based almost entirely upon observed patterns of extinction of species on mountain tops

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(Brown 1971; Patterson 1984), forest (Terborgh & Winter 1980; Newmark 1991; Kattan et al. 1994) and urban habitat fragments (Soulé et al. 1988; Bolger et al. 1991), man-made islands (Willis 1974; Karr 1982), and land-bridge islands (Diamond 1972; Terborgh 1974; Case 1975; Wilcox 1978; Heaney 1984). Very few studies (Weisbrod 1979; Newmark 1987, 1995) have examined patterns of extinction of species across a series of protected areas.

Tanzanian national parks and related reserves contain some of the most diverse and impressive assemblages of large mammals worldwide. Unfortunately, many of the protected areas in Tanzania, as elsewhere in the world, are becoming increasingly insularized as a result of human settlement, agricultural cultivation, and the active elimination of wildlife on lands adjacent to the parks. In recent years human populations have grown at rates as high as 5–15% per year in certain regions adjacent to parks (Kurji 1981; Malpas & Perkins 1986; Campbell & Hofer 1995). The smaller parks in northern Tanzania are now nearly surrounded by human settlements and agricultural cultivation (Fig. 1).

Several former studies (Soulé et al. 1979; East 1981, 1983; Western & Ssemakula 1981; Burkey 1994) have attempted to estimate the proportion of mammal species that may be lost in the future in East African reserves as a result of their increasing insularization. Although all of these studies predicted that Eastern African reserves will lose species as they become increasingly insularized, there has been less agreement as to the magnitude of the loss. The debate is due in large part to the different ap-

proaches that have been taken to estimating rates of extinction. Soulé et al. (1979) and Burkey (1994) extrapolated post-Pleistocene extinction rates for mammals on seven and five islands, respectively, in the Sunda Shelf in southeast Asia and East African reserves. In contrast, Western and Ssemakula (1981) compared species-area relationships for reserves with species-area relationships for ecosystems in East Africa. Finally, East (1981, 1983) estimated the number of species within East African reserves with populations below a certain value.

The purpose of this study is twofold. First, I examine whether patterns of extinction of large mammals in Tanzanian parks are consistent with one prediction of island biogeography theory that habitat islands created by the fragmentation of continental regions should experience rates of extinction inversely proportional to their size. Second, I compare observed patterns of persistence to earlier predicted patterns of persistence for large mammals in East African reserves.

Methods

Parks

I examined the local extinction of mammals in six parks and park assemblages in Tanzania: Arusha, Kilimanjaro, Lake Manyara, Ruaha, and Tarangire National Parks and Serengeti National Park–Ngorongoro Conservation Area (Fig. 1). Serengeti National Park and Ngorongoro Conservation Area were considered a single park assemblage

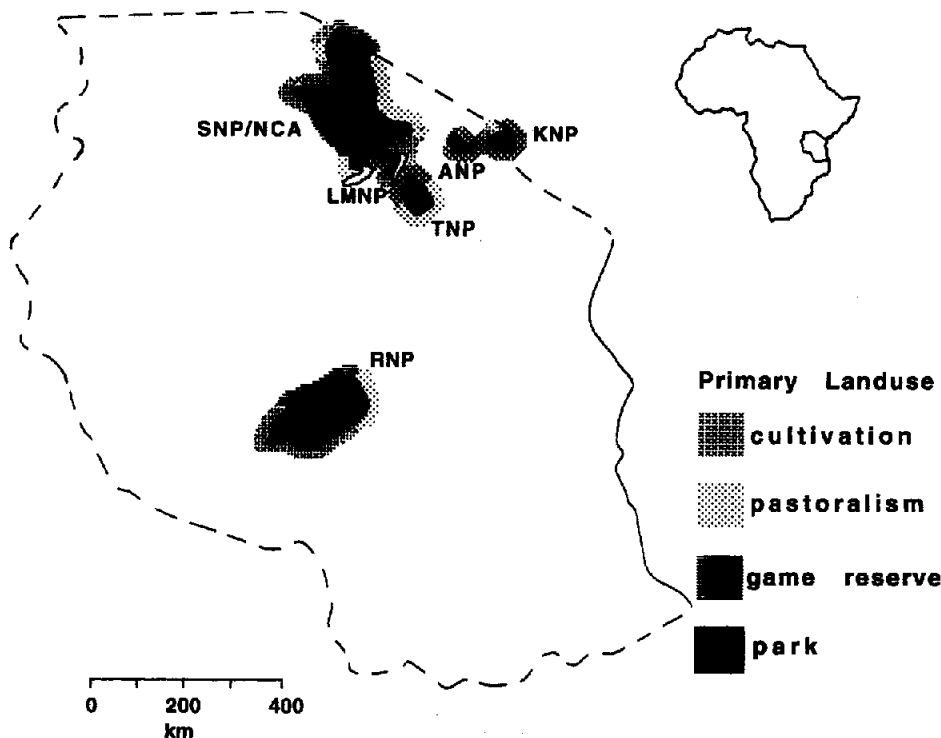


Figure 1. Map showing location in Tanzania of Kilimanjaro (KNP), Arusha (ANP), Lake Manyara (LMNP), Tarangire (TNP), Ruaha (RNP) National Parks, and Serengeti National Park/Ngorongoro Conservation Area (SNP/NCA), and primary land use immediately adjacent to these parks.

Table 1. Biogeographic characteristics of six Tanzanian parks and locally extinct species.

Park	Area (km ²)	Length of protection of mammal community (years)	Number of species found historically ^a	Number of species found currently ^a	Locally extinct species	Date of last reported sighting	Source
Lake Manyara	100 ^b	36	35	33	mountain reedbeek (<i>Redunca fulvorufula</i>) Coke's hartebeest (<i>Alcelaphus buselaphus</i>)	1983 1984	H. H. T. Prins, personal communication H. H. T. Prins, M. Burgengo, I. Douglas-Hamilton, personal communications
Arusha	137	35	26	25	stencbok (<i>Raphicerus campestris</i>)	1967	Vesey-Fitzgerald 1967; Tanzania National Parks 1969
Kilimanjaro	1834 ^c	83	23	21	Klipspringer (<i>Oreotragus oreotragus</i>) ^d mountain reedbeek (<i>Redunca fulvorufula</i>) ^d	1944 1965 1974	Gillman 1923; Miller 1933; Moreau 1944 Moreau 1944; Swynnerton 1949; Swynnerton & Hayman 1951; Child 1965 Lamprey 1963; Tanzania National Parks 1974
Tarangire Ruaha	2600 12950	38 44	41 39	40 39	roan antelope (<i>Hippotragus equinus</i>)		
Serengeti-Ngorongoro Conservation Area	23051	55	49	49			

^a Diurnally or crepuscularly active species within the orders Primates, Carnivora, Proboscidea, Artiodactyla, and Perissodactyla.

^b Includes only the terrestrial portion of the park.

^c Includes all of the montane forest and higher elevational habitats within Kilimanjaro National Park/Game/Forest Reserve.

^d Local extinction formerly reported in Newmark et al. 1991.

because they are contiguous. All six parks and the park assemblage were protected areas before being declared national parks. Thus, the length of protection of the wildlife within the parks has been longer than the actual administrative age of the parks. In addition, the boundaries of several parks have been expanded over time. In calculating the rate of extinction, therefore, I used the length of protection of the entire community of mammals found currently within the parks as a metric of time since isolation (Table 1).

Although this metric is not an exact measurement of time of isolation, because the parks are surrounded by a dynamic matrix of human modified habitat and activities, the length of protection of the wildlife within existing national parks does coincide closely with the length of isolation for nearly all of the species I have included in the analysis for the following reasons. First, the initiation of extensive habitat modification on lands adjacent to the parks occurred nearly simultaneously with the protection of the parks as a result of indigenous peoples who formerly lived within the parks being displaced to regions immediately adjacent to and outside of the parks (Tanganyika National Park 1961; Savidge 1968; Arhen 1985; Neumann 1992). Second, as a result of population pressures in many areas in Tanzania throughout this century, regions adjacent to many parks in Tanzania were quickly settled following establishment of protected areas (Barnes & Douglas-Hamilton 1982; Yeager & Miller 1986; Mwangeni 1992). Third, as a result of wildlife-control measures by local farmers and governmental agencies on agricultural lands adjacent to the parks and of extensive hunting of wildlife, both legal and illegal, on these same lands, virtually all of the large mammals that formerly resided year-round immediately adjacent to the parks have disappeared following the establishment of the parks (Yeager & Miller 1986; Kinloch 1988; Newmark et al. 1991, 1994; Mwangeni 1992; Campbell & Hofer 1995). The exception to this pattern is large mammals that reside year-round within adjacent game reserves.

I examined patterns of extinction in relationship to the legal area of existing national parks and conservation areas (Ngorongoro) in Tanzania because both the historical and current status of large mammals within these protected areas are considerably better documented than in adjacent game reserves. The one exception is Kilimanjaro National Park, for which I have included all of the montane forest and higher elevational habitats on Mount Kilimanjaro as the "legal" area of this park, even though portions of the montane forest are managed as both a game and a forest reserve. Former mammalian surveys on Mount Kilimanjaro have previously used the montane forest as a natural boundary in describing the fauna (Johnston 1886; Moreau 1944; Child 1965; Newmark et al. 1991).

I would have preferred to have included additional East African parks/and park assemblages in this study,

but this would have required the inclusion of parks in neighboring countries; problems associated with logistics and the frequent crossing of international borders unfortunately precluded this.

Documentation of Extinctions

I determined the number of extinctions of species within each park by comparing the historical status of a species with its current status. I documented the historical status of a species within a park by reviewing the literature and interviewing long-term resident scientists, park managers, and tour operators. I determined the current status of a species within a park through field surveys and by interviewing resident scientists, park managers, and tour operators as to sightings of rare and "missing" mammals. Foot and road surveys (diurnal and nocturnal using a spotlight) for "missing" mammals in the parks were conducted over an 8-year period beginning in February 1988. I conducted approximately 1200 hours of diurnal road surveys, 125 hours of nocturnal road surveys, and 130 hours of foot surveys between February 1988 and October 1995. The foot surveys focused on regions of the parks where extinct species had been formerly sighted. Over one-half of the field surveys were conducted in Arusha and Lake Manyara National Parks because these two parks have experienced the highest rates of extinction of large mammals and the dates of last sighting for extinct species are the most recent there (Table 1).

I restricted the analysis to species that are either diurnally or crepuscularly active within the orders Primates, Carnivora, Proboscidea, Artiodactyla, and Perissodactyla. These species tend to be large (median body size = 31.88 kg, range 0.28–3500 kg) and therefore relatively conspicuous. I excluded nocturnally active species from the analysis because of the greater difficulty in documenting both their historical and current status. I also excluded from the analysis transient species known to spend less than 3 months on average per year within a park. Finally, I excluded any species known from only a single record within a park.

I assumed an extinction event if a species was not sighted for a minimum of 10 years as of 1995 within the current legal boundaries of a park or park assemblage. Any extinction that could be attributed directly to commercial poaching within the parks was excluded; thus, the exclusion of the extinction of black rhinoceros (*Diceros bicornis*) in Arusha, Kilimanjaro, Lake Manyara, Tarangire, and Ruaha National Parks.

Statistical Analysis

I assumed that the extinction rate of mammals in Tanzanian parks took the following form:

$$dS/dt = -k_n S^n,$$

where k_n is the extinction parameter, n is an integer exponent defining the shape of the extinction curve, S is species number, and t is the length of protection. The form of the model will vary with the choice of n . I assumed n was equal to either 1, 2, 3, or 4 and solved for k following Richman et al. (1988). The S^1 model assumes that the per-species rate of extinction is constant, whereas the S^2 , S^3 , and S^4 models assume that the per-species rate of extinction varies as a function of species richness. Under these latter models the role of interspecific competition is incorporated. As competitors become extinct, the per-species rate of extinction for surviving species decreases (Terborgh 1974; Soulé et al. 1979).

Results

Patterns of Extinction

During the last 35–83 years, six species of large diurnal mammals have become locally extinct in the six Tanzanian parks I surveyed (Table 1). All locally extinct species are within the order Artiodactyla.

The rate of local extinction of mammal species as expressed by the extinction coefficient k is significantly and inversely related to log park area for both the S^1 model ($r = 0.93$, $p < 0.007$; Fig. 2) and the S^2 model ($r = 0.86$, $p < .026$). The extinction coefficient k is insignificantly correlated ($p > 0.05$) with log park area for the S^3 and S^4 models. The inverse relationship between the extinction coefficient k and log park area for the S^1 and S^2 models indicates that the rate of extinction of mammals following their protection in Tanzanian parks is higher in the smaller parks.

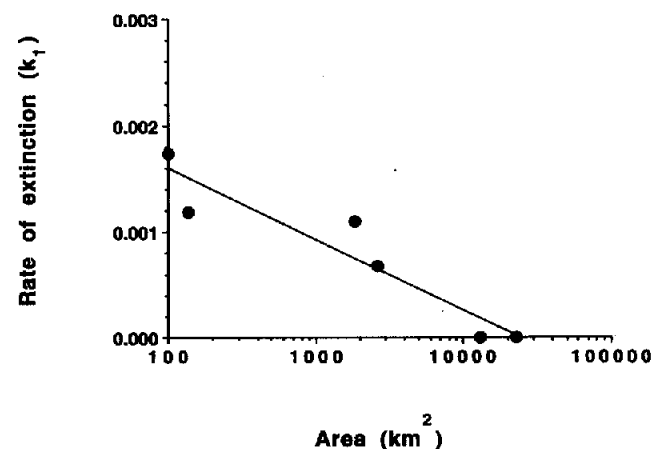


Figure 2. Relationship between the rate of extinction (k_e) and park area. The straight line shows the relationship $Y = 0.003 - 0.001(\log \text{Area})$ ($p < 0.007$).

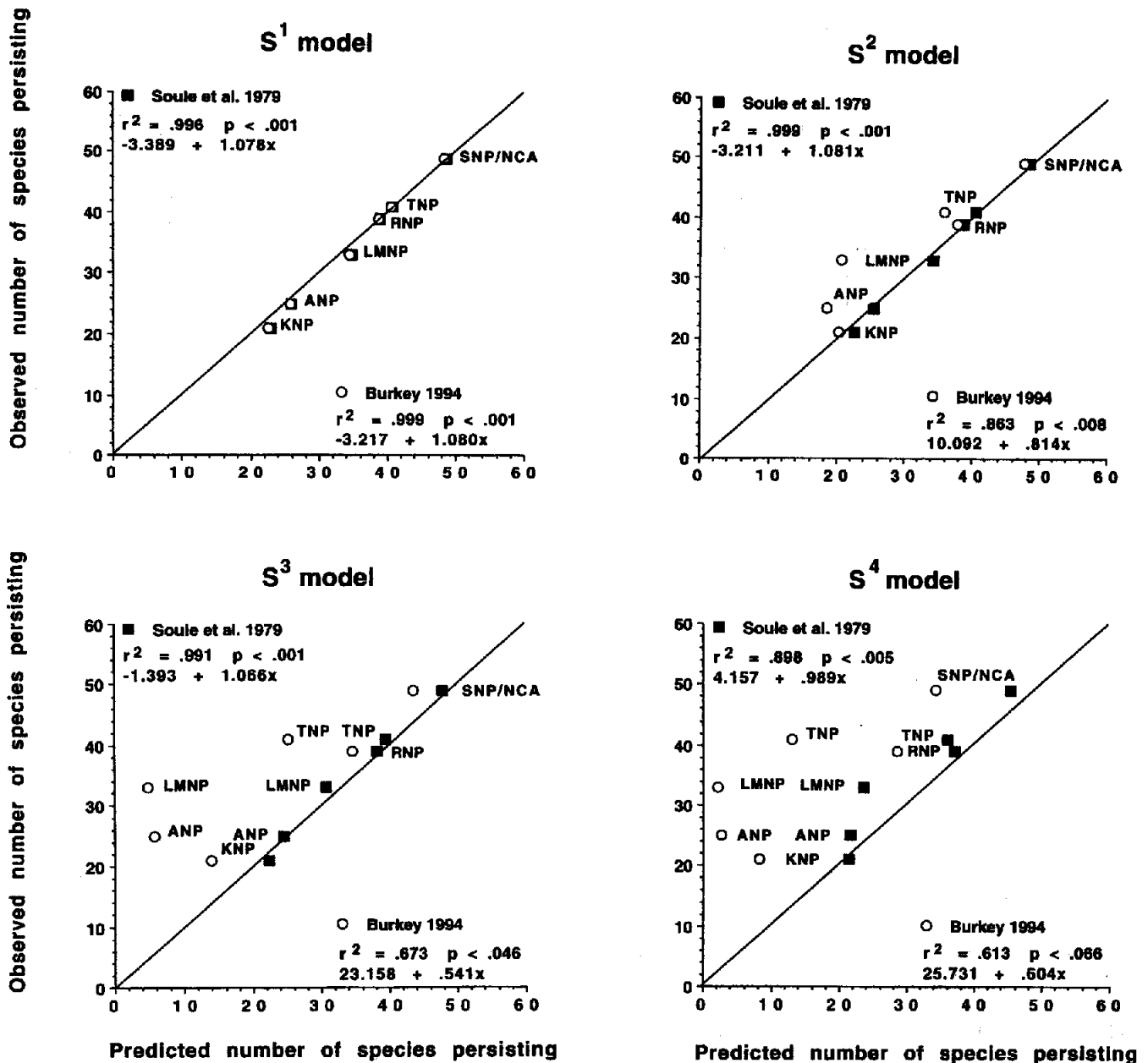


Figure 3. The predicted number of species persisting in six Tanzanian parks based upon the S^1 , S^2 , S^3 , and S^4 extinction models of Soule et al. (1979) and Burkey (1994) is plotted against the observed number of species persisting. The abbreviations for each of the parks follow Fig. 1. The coefficient of determination, level of significance, and linear equation describing the fit between predicted and observed number of species persisting is shown for each of the extinction models.

Although I limited the analysis to species that are either diurnally or crepuscularly active because the historical and current status of these mammals is better documented than for nocturnally active species, the inclusion of these latter species increases the proportion of variation in the rate of extinction of mammals that is explained by park area for both the S^1 ($r^2 = 0.98$, $p < 0.001$) and S^2 ($r^2 = 0.90$, $p < 0.004$) models.

Similarly, I have limited the analysis to the legal area of existing national parks and conservation areas because the historical and current status of large mammals in these protected areas is better documented than within adjacent game reserves. As with the inclusion of nocturnal mammals in the analysis, including adjacent game reserves in defining the area that is legally protected increases the proportion of variation in the rate of ex-

tion of mammals that is explained by area for both the S^1 ($r^2 = 0.95$, $p < 0.002$) and S^2 ($r^2 = 0.78$, $p < 0.02$) models.

Observed and Predicted Patterns of Persistence

A debate has emerged in recent years over the size of the faunal collapse that should occur in East African protected areas as they become increasingly insularized (Soulé et al. 1979; East 1981, 1983; Western & Ssemakula 1981; Burkey 1994). But a comparison of the predictions of the various models to the observed patterns of persistence of mammals in Tanzanian parks is possible for only those models (Soulé et al. 1979; Burkey 1994) that have explicitly incorporated time. The extinction models of Soulé et al. (1979) and Burkey (1994) propose that the rate of extinction of mammals in East African reserves should take the following form: $dS/dt = -k_n S^n$, where S is species number and k is an extinction coefficient calibrated from data on post-Pleistocene extinctions of large mammals on seven and five islands, respectively, in the Sunda Shelf in southeast Asia.

The predictions of species persistence in Tanzanian parks based upon the S^1 model of Soulé et al. (1979) and Burkey (1994) and the S^2 and S^3 models of Soulé et al. (1979) closely match the observed pattern of persistence of mammals in Tanzanian parks (Fig. 3).

Discussion

The inverse relationship between the rate of extinction of mammals in Tanzanian parks and park area is consistent with a prediction of the theory of island biogeography that habitat islands created by fragmentation of continental regions should lose species at a rate proportional to their size. This pattern of extinction strongly suggests that the increasing insularization of the parks as a result of habitat alteration and the active elimination of wildlife on adjacent lands has been an important contributing factor in the local extinction of large mammals in Tanzanian parks.

It is possible, however, given the small number of parks in this study (six), that the inverse relationship between the rate of extinction and park area may be spurious, particularly if species number (S) and length of isolation (T) covary with park area (A). Yet for the six Tanzanian parks included in this study, species number (S) and length of isolation (T) are insignificantly correlated ($p > 0.05$) with park area (A). The insignificant positive correlation between species number and park area verifies former results of Miller and Harris (1977) and Western and Ssemakula (1981), who compared large-mammal species numbers with park area in 13 and 19 East African reserves, respectively. Thus, I conclude that the in-

verse relationship between park area and the rate of extinction of mammals in Tanzanian parks is robust.

Although a number of workers have questioned the utility of the extinction models that Soulé et al. (1979) proposed for large mammals in East African reserves because of the size of their associated confidence intervals (Boecklen & Gotelli 1984; Boecklen & Simberloff 1986), the S^1 , S^2 , and S^3 models of Soulé et al. (1979) accurately describe, at least in the short term, the observed patterns of persistence of large mammals in Tanzanian parks. The degree to which the predicted number of species persisting in Tanzanian parks matches the observed number is somewhat surprising given that the extinction coefficients of the models employed by Soulé et al. (1979) and Burkey (1994) were calibrated from data on post-Pleistocene extinctions of mammals in the Malay peninsula. This result thus raises an interesting question of how invariant are mammalian rates of extinction as a result of insularization through space and time and across taxa. This result, also along with the inverse relationship between park area and the rate of extinction of mammals in Tanzanian parks, strongly suggest that earlier concerns (Burgman et al. 1988) about the practical utility of island biogeographic models to questions of management and conservation of wildlife populations in East Africa are unfounded.

But could alternative explanations for the insularization of the parks explain the observed patterns of extinction of large mammals in Tanzanian parks? Could human disturbance—specifically poaching—rather than insularization be responsible for the observed patterns of extinction? Both commercial and subsistence poaching have occurred at some point in all of the parks. Commercial poaching in Tanzania is conducted by individuals using primarily firearms and is focused upon a selected group of species with high monetary value (e.g., black rhinoceros, elephant [*Loxodonta africana*]). In contrast, subsistence poaching is conducted by local people using principally snares, which are a comparatively nondiscriminatory harvesting technique. As a result of the differences in the harvesting methods and intensity of hunting pressure, the adverse impact of commercial poaching on mammal populations in parks is considerably greater than that of subsistence poaching (Arcese et al. 1995; Campbell & Hofer 1995). I have excluded from the analysis any local extinction that could be related directly to commercial poaching; it is possible, however, that subsistence poaching may have been one of a variety of factors (e.g., disease, inbreeding depression, demographic accidents, and drought) that could have adversely affected insularized populations.

It is important to note that the most intensive levels of subsistence poaching have occurred historically in the two largest parks in this study (Serengeti-Ngorongoro and Ruaha), which have not experienced any local extinctions of noncommercially valuable species. On the

other hand, subsistence poaching of wildlife has historically been a comparatively minor activity in the four smaller parks in which local extinctions of large mammals have occurred. I conclude that although subsistence poaching may have been one of a variety of factors that could have adversely affected locally extinct species in the past, it has not been the predominant determinant of their extinction.

Given the current population growth rate in Tanzania of 3.0% per year (World Bank 1992), it is highly probable that protected areas in Tanzania will become further isolated. The smaller parks will probably continue to experience the highest rates of species loss in the near future. Species that are both rare and incapable and/or reluctant to use human-modified habitat adjacent to the parks will be particularly prone to future extinction within the parks.

One potential means of reducing the rate of loss of species as well as increasing the likelihood of species recolonizing the parks is to link the parks in northern Tanzania with a system of wildlife corridors (Preston 1962; Diamond 1972; Wilson & Willis 1975; Harris 1984; Noss 1992). Nearly all of the locally extinct species are found within neighboring parks. But wildlife corridors will be effective in reducing the loss of species and in increasing the likelihood of species recolonizing the parks only if they are designed specifically to promote the movement and dispersal of these species (Newmark 1993). Although concerns have been raised about the possibility of corridors transmitting disease, predators, noxious or exotic plants and animals, and genetic outbreeding depression (Simberloff & Cox 1987), practically it should be much easier to create temporary barriers to prohibit the movement of species or the transmission of disease than to establish corridors after critical habitat is lost (Newmark 1993).

The potential utility of wildlife corridors in reducing the rate of loss of species as well as the adverse effects of isolation on large-mammal populations is illustrated by the recent recolonization of Lake Manyara National Park by eland (*Taurotragus oryx*). Lake Manyara, which borders the eastern edge of the park (Fig. 1) and is a significant barrier to the movement of large mammals, dried up entirely with the exception of a few isolated pockets of water at the end of 1993. Eland, last sighted in 1983, recolonized the park in December 1993 by crossing the dry lake bed (I. M. Lejora, personal communication).

Unfortunately, the opportunity to establish and connect many of the smaller northern national parks in Tanzania with wildlife corridors is probably limited to the next 5 years, given the rapid rate at which many of the lands adjacent to the smaller parks are being settled and cultivated. After this period the political and economic costs of establishing wildlife corridors between the smaller parks may be prohibitive.

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