

FAUNAL COLLAPSE IN EAST AFRICAN GAME RESERVES REVISITED

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Abstract

Soulé *et al.* (Biol. Conserv., 1979, 15, 259–72) predicted that without intensive management, East African game reserves would lose a large proportion of their large mammal faunas if they became completely insularized (isolated from other habitat areas with healthy wildlife populations). They based their predictions on the loss of large mammal species from islands in the Malay archipelago following their insularization at the end of the Pleistocene. This paper considers the difficulty of estimating extinction rates from existing data and the paucity of data on the relationship between extinction rates and area. Re-analysing the Malay archipelago data, I find that insularized reserves may lose species even more rapidly than Soulé *et al.* predicted.

Keywords: extinction, nature reserves, habitat fragmentation, large mammals, wildlife management.

INTRODUCTION

In a rare application of island biogeography theory to concrete management situations, Soulé *et al.* (1979) predicted a severe loss of large mammal species from insularized East African wildlife reserves under a management regime of 'benign neglect' (the absence of either destructive or supportive human intervention).

Soulé *et al.* suggested the following four models of extinction rates: (1) $dS/dt = -k_1S$; (2) $dS/dt = -k_2S^2$; (3) $dS/dt = -k_3S^3$; (4) $dS/dt = -k_4S^4$, where S is the number of species. The extinction coefficients, k_1 through k_4 , are calibrated from data on mammalian species loss on islands in the Malay archipelago following the severing of the land-bridge at the end of the Pleistocene. I will refer to k_1 through k_4 as per species extinction rates, though this usage is precise only in the case of k_1 .

The authors are of course aware of the problems associated with calibrating models for the relaxation of East African mammal faunas with data from Malay faunas, but they may be correct that it is the best we can do at present. Assuming that the endeavour is worthwhile, there are some problems with their analysis. Unfortunately, re-analysing the data to correct these problems yields predictions for African wildlife which are much more dire than those made by Soulé *et al.*

METHODS

The fact that the numbers of species, S_0 , present on islands of the Malay archipelago at the time of isolation are not known creates some initial problems in estimating rates of species loss. Soulé *et al.* use the relative invariance of the slopes, z , for continental species area curves to estimate S_0 , by calibrating the model $S=cA^z$ with the present number of species on the Malaysian peninsula (S is the number of species, A is area, and they use $z = 0.14$ as an intermediate value for the slope of continental species–area curves). This may be unfortunate, as peninsulas often have relatively low species abundances (Williamson, 1981), and there is no guarantee that species–area curves had the same slopes 10 000 years ago as they do today. The Malaysian peninsula is smaller than some of the islands in the study and may have lost some of the species present at the end of the Pleistocene. Furthermore, the islands may have sampled fauna from a wide region as animals moved to higher ground, so estimating S_0 from a continental species–area curve may lead to underestimated extinction rates. The actual areas of the islands have also varied widely since their isolation. The models treat all species as if they can be lumped together to yield a meaningful measure of per species extinction rates across faunas and spatial scales, although species are known to vary widely in their extinction proneness and area requirements (Diamond, 1984). Let us assume, however, that this method of estimating extinction rates works reasonably well. In other island faunas, it is astonishing how large a proportion of the variation in similarly estimated extinction rates can be accounted for by island area (Burkey, in press). The per species extinction rates must be assumed to remain constant through time.

Soulé *et al.* use linear regressions of $\log(\text{extinction rates})$ vs. $\log(\text{area})$ to interpolate extinction rates on 'islands' of different areas. This is unfortunate for a number of reasons. First, \log transformations of the dependent variable tend to inflate the R^2 values. Secondly, despite this inflation, the R^2 obtained are very low ($R^2 = 0.231$ for model 1 through $R^2 = 0.426$ for model 4). Thirdly, an exponential function fitted to untransformed rates and areas yields a much better fit than a linear equation fitted to the \log – \log transformed

data ($R^2 = 0.416$ for model 1). Finally, the two smallest islands in the sample, Penang and Langkawi, are very close to the Malaysian mainland (c. 2 and 15 km, respectively). The extinction rates estimated for these two islands are conspicuously low, which suggests a rescue effect (Brown & Kodric-Brown, 1977), and probably reflects multiple recolonization events and a more recent separation from the mainland. Soulé *et al.* assumed that all islands were isolated c. 10 000 years ago, but the water between the Malaysian peninsula and Penang is less than 8 m deep, for Langkawi less than 15 m, while the others are isolated by depths greater than 40 m (Defence Mapping Agency (US), Omega Plotting Charts 71005 (1992) and 71033 (1986)). Hence, Penang and Langkawi were most likely isolated 2000–3000 years later than the other islands in the sample (see Bard *et al.*, 1990; Pirazzoli, 1991). On the other hand, Bangka probably separated from Sumatra at about the same time as Langkawi separated from the mainland. While improved estimates of the time since isolation will improve estimates of extinction rates, the rescue effect is probably highly non-linear and very difficult to correct for. (Soulé *et al.* noted the relatively high species richness of Penang and Langkawi and their proximity to the mainland.)

I reconsider Soulé *et al.*'s regression of extinction coefficients against area and redo their analysis after removing Penang and Langkawi from the sample of islands. The coefficients are estimated from $k_1 = \frac{\ln(S_p/S_i)}{T}$, $k_2 = \frac{\frac{1}{S_p} - \frac{1}{S_i}}{T}$, $k_3 = \frac{\frac{1}{S_p} - \frac{1}{S_i}}{2T}$, $k_4 = \frac{\frac{1}{S_p} - \frac{1}{S_i}}{3T}$, where T is set to 10 000 years (assumed time since isolation) and S_p , the 'present' number of species on each island, was estimated by Soulé *et al.*, following Medway (1969). I fit linear, exponential, and logarithmic functions to these estimates against area (or log area) for the remaining islands, selecting the one which explains the greatest proportion of the variation.

RESULTS

Figure 1 shows the regression of k_1 (the per species extinction rate from model 1) against area, fitted by Soulé *et al.* for seven Malay archipelago islands. Notice the poor fit due to the uncharacteristically low extinction rates of the two smallest islands, Penang and Langkawi. The relationship is not monotonically decreasing as one would expect, all else being equal, but rather hump-shaped. A quadratic equation fitted to the extinction rates as a function of area yields more than a 3-fold increase in the proportion of the variation explained by the regression (Fig. 1, grey curve). The quadratic fits even better if the y-axis is not log-transformed ($k_1 = -4.27 \times 10^{-4} + 2.93 \times 10^{-4} x - 3.71 \times 10^{-5} x^2$, $R^2 = 0.84$).

Populations that we attempt to manage for conservation now and in the future may not have any 'mainland' source populations, and the relevance of results from islands with outside recolonization may be reduced (Terborgh, 1976; Cole, 1981). I propose that the

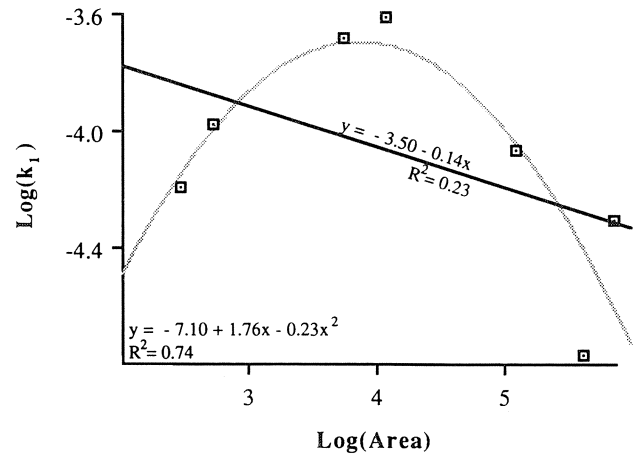


Fig. 1. The regression of per species extinction rate (per year, from model 1: $(dS/dt = -k_1S)$ against area (km^2) for mammals on Malay archipelago islands; used by Soulé *et al.* (1979) to calibrate one of four models of species persistence in East African wildlife reserves (solid line). The islands are, in order of increasing area, Penang, Langkawi, Bali, Bangka, Java, Sumatra, and Borneo. The goodness of fit (R^2) is greatly improved by fitting a quadratic equation (grey curve).

two islands closest to the mainland should be removed from the sample since their extinction rates are probably vastly underestimated, and since they are responsible for the poor fit of monotonically decreasing functions in area. Figure 2 shows the new regression of k_1 (the per species rate of extinction, model 1) against area for the remaining islands. The regression is not sensitive to the estimated time since isolation for the different islands, so no attempt has been made to use more accurate estimates than the 10 000 years assumed by Soulé *et al.*

Removal of Penang and Langkawi yields substantially steeper regressions of per species extinction rates

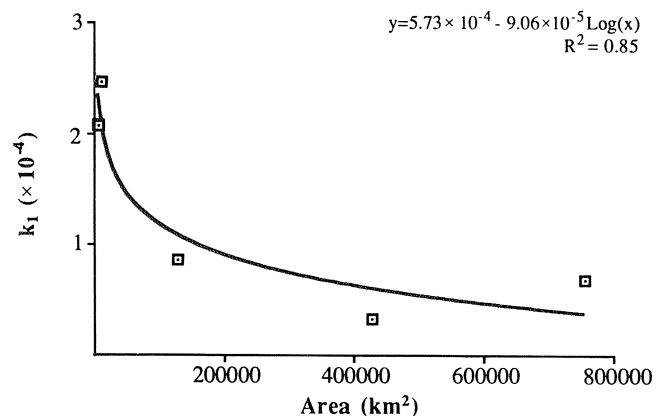


Fig. 2. Alternative regression of per species extinction rate (per year, from model 1) against area for mammals on Malay archipelago islands; used to re-calibrate one of four models of species persistence in East African wildlife reserves. The two smallest islands, Penang and Langkawi, have been excluded from the analysis due to their close proximity to the Malaysian peninsula mainland. Extinction rates for Borneo and Sumatra have been re-estimated, and are higher than those used by Soulé *et al.* (see main text and Fig. 1). Regressions for the other three models are listed in the caption to Table 1.

Table 1. Biogeographic data from Soulé *et al.* (1979), and recalculated number of large mammal species remaining 50, 500, and 5000 years after isolation — for East African wildlife reserves within the range of areas of the Malay archipelago islands on which regressions were based.

k_1 , k_2 , k_3 , and k_4 are re-estimated extinction rates based on the four different models proposed by Soulé *et al.* The re-estimated extinction rates as a function of area are: $k_1 = 0.00057 - 0.00009 \text{ Log}(\text{area})$, $R^2 = 0.85$; $k_2 = 0.015 \times 10^{-0.72 \text{ Log}(\text{area})}$, $R^2 = 0.88$; $k_3 = 0.13 \times 10^{-1.17 \text{ Log}(\text{area})}$, $R^2 = 0.90$ and $k_4 = 1.97 \times 10^{-1.67 \text{ Log}(\text{area})}$, $R^2 = 0.91$ (all logarithms to base 10). Soulé *et al.* suggest that models 2 and 3 are the most realistic. Their estimates are in parentheses.

Reserve	Area (km ²)	Number of large mammal species	Extinction rates				Years after isolation	Number of species remaining			
			k_1	k_2	k_3	k_4		1	2	3	4
Tsavo	20808	63	0.00018	1.2×10^{-5}	1.1×10^{-6}	1.2×10^{-7}	50	62 (63)	61 (62)	52 (60)	35 (54)
							500	58 (61)	46 (55)	27 (45)	17 (34)
							5000	25 (42)	13 (28)	9 (20)	8 (16)
Serengeti	14504	70	0.00019	1.5×10^{-5}	1.7×10^{-6}	2.3×10^{-7}	50	69 (70)	66 (69)	52 (66)	30 (56)
							500	63 (67)	46 (60)	23 (45)	14 (32)
							5000	26 (46)	11 (27)	8 (18)	7 (15)
Ruaha	12950	49	0.00020	1.6×10^{-5}	1.9×10^{-6}	2.7×10^{-7}	50	49 (49)	47 (48)	40 (47)	27 (44)
							500	44 (47)	35 (44)	21 (37)	13 (29)
							5000	18 (32)	10 (23)	7 (17)	6 (15)
Ngorongoro	6475	40	0.00022	2.7×10^{-5}	4.4×10^{-6}	8.7×10^{-7}	50	40 (40)	38 (40)	31 (39)	19 (36)
							500	36 (38)	26 (36)	14 (31)	9 (25)
							5000	13 (25)	6 (18)	5 (14)	4 (13)
Serengeti-Mara	16317	73	0.00019	1.4×10^{-5}	1.5×10^{-6}	1.9×10^{-7}	50	72 (73)	69 (72)	55 (68)	32 (58)
							500	66 (70)	48 (63)	24 (47)	15 (33)
							5000	28 (48)	12 (28)	8 (19)	7 (16)

versus area than the ones used by Soulé *et al.* Furthermore, from their continental species area equation, the estimated number of species initially present on Borneo and Sumatra should be 65 and 60, respectively — not 51 for both as calculated by Soulé *et al.*, causing them to underestimate the extinction rates on these islands. However, with the more flexible curve-fitting functions used in the present analysis, this underestimation has little effect on the predicted species loss in East African nature reserves since Borneo and Sumatra are so much larger than existing reserves. It is unfortunate that we are essentially down to three data points which affect estimates of extinction rates at the spatial scale relevant to our larger nature reserves.

Table 1 shows the re-estimated number of large mammal species over time, in the five largest East African reserves studied by Soulé *et al.* — following their procedure but based on the new regressions. The re-estimated numbers of species remaining in the reserves as a function of time are much lower than the original estimates. Many estimates are reduced by 50% or more after 500 years, and substantial losses could occur within 50 years. The qualitative result, that reserves may lose large species rapidly if they become insularized, is of course more important than the actual estimates of remaining species through time.

DISCUSSION

As Soulé *et al.* point out, the assumption of benign neglect is for many species overly optimistic — witness the decimation of elephant and rhino populations

throughout eastern and southern Africa in the 1980s and 1990s. On the other hand, the treatment of large mammal species on Malay archipelago islands, such as Java, in the Recent has not either been entirely benign. Clearly, the extrapolation from Malay archipelago mammals in the Holocene to East African mammals in the third millennium AD should be regarded with healthy scepticism. There are numerous reasons why 'no park is an island' (see Janzen, 1986; Laurance, 1991). Furthermore, due to the great variation in size among islands in the Malay sample, there is very little replication at the spatial scale of East African wildlife reserves. More, better, and more appropriate data are needed, as are more precise extinction models. The present results may have some applicability to existing and potential nature reserves on Borneo, Sumatra, and other parts of the region, but this exercise serves perhaps primarily to emphasize our great uncertainty about the size of areas needed to prevent the extinction of species in habitats fragmented by humans.

If the data from the Malay archipelago have any predictive value for reserves elsewhere, the re-analysis suggests, more strongly than the analysis by Soulé *et al.*, that wildlife reserves must be substantially larger than those presently established if they are to preserve their species assemblages (Soulé *et al.* did emphasize that their predictions of species losses in East African nature reserves were conservative). Even large reserves like the Selous in Tanzania (51 200 km²) would lose a large part of their large mammal faunas in a few centuries following complete insularization. Alternatively, intensive management efforts must be implemented.

The latter is probably the more expensive alternative. It is certainly less reliable. Connecting existing parks with dispersal corridors, and preventing complete isolation of parks like Serengeti and Ngorongoro from each other and other habitat areas, may be relatively cheap, viable options in some cases (but see Simberloff *et al.*, 1992; Hess, 1994). Migratory species like the wildebeest must be given special consideration if reserves become true isolates. In light of the troubling estimates of species loss from existing parks, present efforts to join parks in Angola, Botswana, Namibia, Zambia, and Zimbabwe into a vast 246 000 km² conservation area (African Wildlife News Service, 1992) are highly laudable. We must make the necessary funds available for land acquisition and management in and around already-established wildlife reserves — not just in Africa but everywhere. Wealthy industrialized nations who have squandered most of their own biological treasures have a special responsibility to help developing countries save theirs before it is too late.

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