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# Time Lag between Deforestation and Bird Extinction in Tropical Forest Fragments

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**Abstract:** *Tropical forests are becoming increasingly fragmented, threatening the survival of the species that depend on them. Small, isolated forest fragments will lose some of their original species. What is uncertain is how long this process of faunal relaxation will take. We compiled data on birds in five tropical forest fragments in Kakamega Forest, Kenya, of known date of isolation. We then predicted the original and eventual species richness of these fragments and, from this difference, the eventual species losses. Expressing the losses to date as a fraction of eventual losses suggests that faunal relaxation approximates an exponential decay with a half-life of approximately 50 years for fragments of roughly 1000 ha. In other words, in the first 50 years after isolation, tropical forest fragments of this size suffer half of the total number of extinctions that they are likely to experience. This result sets the time scale over which humanity must take conservation action in fragmented tropical forests, may aid efforts to set priorities, and indicates how high the future global extinction rate will be.*

Espacio Temporal entre la Deforestación y la Extinción de Especies de Aves en Fragmentos de Bosques Tropicales

**Resumen:** *Bosques tropicales se están volviendo cada vez más fragmentados, poniendo en peligro la existencia de las especies que dependen de ellas. Fragmentos pequeños y aislados perderán algunas de sus especies originales. Lo que no es cierto es cuánto tiempo durará este periodo de pérdida faunística. Aquí compilamos datos sobre aves en cinco fragmentos de bosque tropical en el Bosque de Kakamega, Kenya, de las cuales conocemos sus fechas de aislamiento. A continuación, predijimos la pérdida original y eventual de estos fragmentos y, de la diferencia entre estas, la pérdida eventual de especies. Cuando expresamos las pérdidas hasta la fecha como una fracción de pérdidas eventuales, se estima que la pérdida faunística aproxima una decaencia exponencial con una media vida de más o menos 50 años para fragmentos de aproximadamente 1000 ha. En otras palabras, fragmentos de bosque tropical de este tamaño, para los primeros 50 años después de aislamiento, sufren la pérdida de la mitad de las especies de que probablemente perderán. Este resultado establece la escala de tiempo sobre la que debemos tomar acción para proteger bosques tropicales fragmentados. También podrá ayudar esfuerzos para establecer prioridades e indica a que altura llegará la futura extinción global.*

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## Introduction

Deforestation continues apace around the world (Whitmore 1997). In temperate forests, where most clearance

occurred a century ago, we already observe species extinctions (Pimm & Askins 1995). In contrast, there are few confirmed extinctions in the continental tropics (Heywood & Stuart 1992). Large numbers of tropical rainforest species are now listed as threatened by the destruction of their habitat (Baillie & Groombridge 1996). Thus it may be only a matter of time before extinctions occur. This is known as relaxation: the original number of species in the fragmented area eventually relaxes to a new, lower number (Diamond 1972). We ask how long

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this relaxation takes. Knowing the answer will help conservation priorities to be set more efficiently.

One can estimate the time lag following habitat destruction before extinction by employing either of two approaches. The simple one is to find a freshly isolated fragment and then to watch and wait. This is the approach being taken by the Biological Dynamics of Forest Fragments project in the Brazilian Amazon (Bierregaard et al. 1992) and in studies of islands isolated by rising waters following the damming of the Lago Guri, Venezuela (Terborgh et al. 1997). But managers need approximate answers now, not when it is too late to use them to mitigate humanity's current actions. This precipitates an alternative approach.

Our previous work employs the familiar, empirical relationship between the size of an area,  $A$ , and the number of species it contains,  $S$ , to predict how many species should eventually be lost when forest area is reduced. We have two case studies: the Atlantic Forest region of South America (Brooks & Balmford 1996) and the islands of Southeast Asia (Brooks et al. 1997). The global survey of Collar et al. (1994) includes lists of the bird species threatened with extinction in these regions. The predicted numbers of species lost from deforestation closely match these independently compiled totals of threatened species. This match suggests that these threatened species will indeed become extinct in due course and thus that we can predict the eventual species losses.

Our study assesses data for a number of isolated forest fragments of known ages, for which we can estimate the extent to which extinctions have already occurred. Comparing these actual losses to the predictions of eventual loss permits the calculation of how long it will take for tropical forest fragments to suffer bird extinctions.

## Methods

One needs to know how many species survive in the fragment at three (or more) points in time: (1) before isolation (starting point); (2) after relaxation, that is, after every species that is going to become extinct has become extinct (end point); and (3) at least one point in time between the start and end points, which indicates how fast species are being lost.

How can one estimate how many species were present ( $S_{\text{original}}$ ) in the area before it was isolated and how many species will survive in the future ( $S_{\text{fragment}}$ )? If one does not use the "watch and wait" approach, then one has no direct way of counting these species. Historical collections or surveys can provide lists of the total numbers of species ( $S_{\text{total}}$ ) in the larger area ( $A_{\text{total}}$ ), from which only the fragment will eventually survive. They almost certainly, however, do not distinguish the particular area that is now the fragment ( $A_{\text{fragment}}$ ) from the once-continuous habitat ( $A_{\text{total}}$ ) that surrounded it.

Instead, we used the mathematical relationship between the size of an area and the number of species it holds. The derivation of a power function from first principles by Preston (1962) has led to the general acceptance of a form  $S = cA^z$  for this relationship, where  $S$  = species number,  $A$  = area, and  $c$  and  $z$  are constants (Rosenzweig 1995). Our key assertion is that we can predict both  $S_{\text{fragment}}$  and  $S_{\text{original}}$  from the species-area relationship with sufficient accuracy to allow estimations of the time it takes species to be lost.

Surveys of the number of species in progressively larger areas of continuous habitat show that the larger the area surveyed, the more species there will be, but that the relationship is rather weak. Typical  $z$  values for progressively larger areas of continuous habitat are approximately 0.15. We can use this value to estimate  $S_{\text{original}}$ . The ratio of the species in the soon-to-be-isolated fragment to that in the total area of habitat is given by

$$S_{\text{original}}/S_{\text{total}} = (A_{\text{fragment}}/A_{\text{total}})^z. \quad (1)$$

Because we know  $S_{\text{total}}$ ,  $A_{\text{fragment}}$ , and  $A_{\text{total}}$  and take  $z$  to be approximately 0.15, we can rearrange equation 1 to calculate  $S_{\text{original}}$ .

Surveys of numbers of species on isolated islands also show that the larger the area the more species there will be. The relationship is of the same form as equation 1, but the slope is a steeper one,  $z$  being approximately 0.25 (Rosenzweig 1995); there are fewer species for an area of a given size. Such islands have been isolated for so long that one assumes they have reached their equilibrium number of species (Diamond 1972). We can use this relationship with the higher value of  $z$  to estimate  $S_{\text{fragment}}$ :

$$S_{\text{fragment}}/S_{\text{total}} = (A_{\text{fragment}}/A_{\text{total}})^z. \quad (2)$$

These ideas are not new (Brown 1971). Figure 1 depicts relationships of this form with  $z$  at approximately 0.15 (upper curve *B*) and  $z$  at approximately 0.25 (lower curve *C*). The upper curve gives us  $S_{\text{original}}$ , and the lower curve give us  $S_{\text{fragment}}$ .

How good will be estimates derived from these two inevitably uncertain predictions? Consider a special case: when one knows accurately the fauna of an area with well-defined boundaries,  $S_{\text{original}} = S_{\text{total}}$ . In such cases, there is only one uncertain value,  $S_{\text{fragment}}$ . If we can accurately predict species losses from deforestation, we can be confident that our estimates of  $S_{\text{fragment}}$  are reasonable. For eastern North America, a long-deforested region, deforestation exactly predicts the number of extinctions that have already occurred (Pimm & Askins 1995). For two recently deforested regions, insular Southeast Asia (Brooks et al. 1997) and the Atlantic forests of South America (Brooks & Balmford 1996), the formula accurately predicts the numbers of bird species that are deemed "threatened with extinction in the medium term." These calibrations increase confidence that one can predict  $S_{\text{fragment}}$ —the future numbers of species.

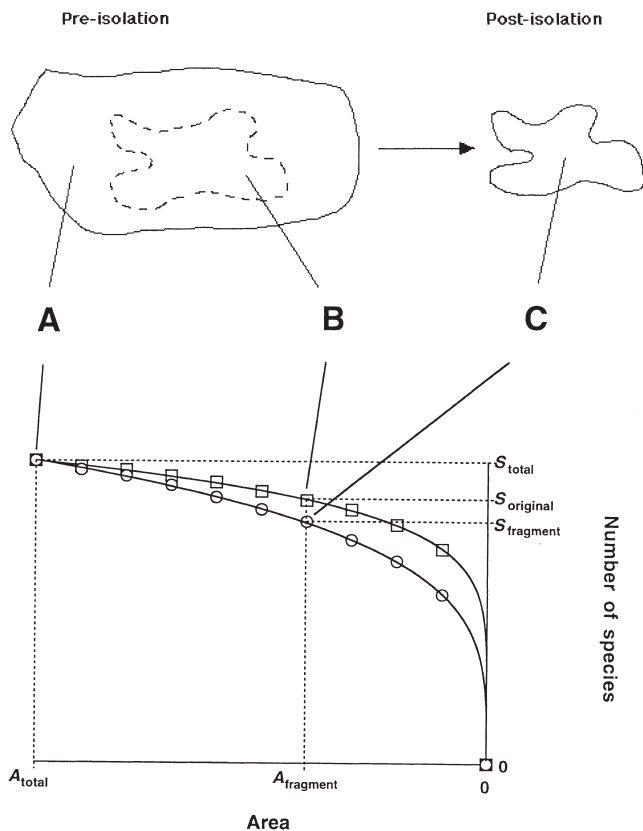


Figure 1. Typical species-area relationships. Larger areas (A) have more species than smaller ones (B, C), and areas that have been long isolated—such as islands—have proportionately fewer species (C) than do equal-sized areas nested within continuous habitat (B). A forest with an area of  $A_{total}$  holds  $S_{total}$  species (A). An area nested within this forest (B), has an area of  $A_{fragment}$  and holds  $S_{original}$  species. After deforestation, the area of  $A_{fragment}$  is all that remains (C). It holds  $S_{original}$  species at the point of deforestation, but over time many of these will become extinct, leaving only  $S_{fragment}$  species.

The  $S_{now}$  value is the easiest to obtain. Through intensive fieldwork, we can count how many species ( $S_{now}$ ) presently survive in the forest fragment at a time ( $t$ ) after fragmentation. This value should fall between the initial number of species  $S_{original}$  and the final number  $S_{fragment}$ . It should not exceed the former. It could be below the latter, in which case it would reject the claim to be able to predict a priori. When it equals the latter, one would predict no further species losses.

We can now combine all the available information to derive a “relaxation index” ( $I$ ), which is the ratio of the number of extinctions yet to occur after time  $t$  to the total number that will eventually occur:

$$I = (S_{now} - S_{fragment}) / (S_{original} - S_{fragment}). \quad (3)$$

Immediately after fragmentation,  $I$  will equal 1, and it will eventually decline to 0. The final step is to assume a particular form for how  $I$  declines with time. We assume that the decline in species is to a first-approximation exponential (Diamond 1972) and therefore that one can characterize it by a fixed time to lose half of the species to be lost. In other words, if in  $T$  years the fragment loses 50% of its species, in another  $T$  years it will lose half of what remains, (25% of the total), and in the next  $T$  years the next half of what remains (12.5% of the total), and so on (Fig. 2). Thus,

$$I = \exp(-k \times t). \quad (4)$$

From this, one can estimate the decay constant,  $k$ , and then, by setting  $I = 0.5$ , the half-life—the time taken to lose half the species that will be eventually lost from the community.

### Kakamega Rainforest, Kenya

We surveyed birds in three different areas of fragmented upland forests in Kenya in 1996. Prior to this, we reviewed the literature, contacted ornithologists who had visited the forests, and compiled forest cover data from satellite imagery, aerial photographs dating back to

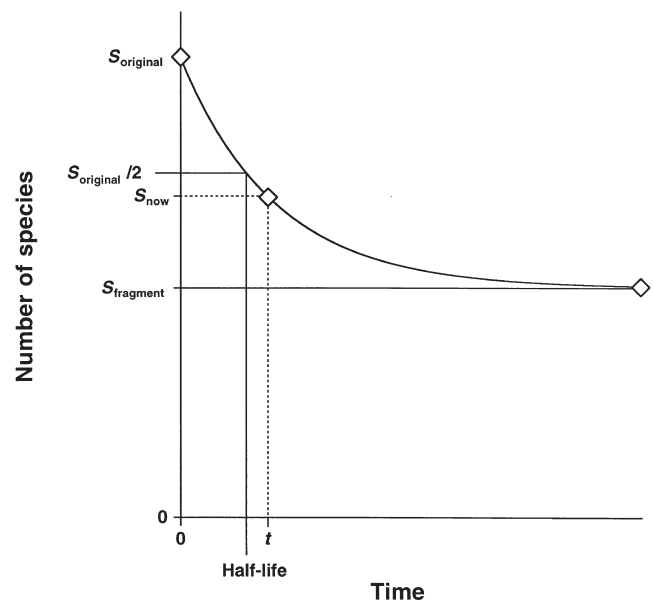


Figure 2. Exponential loss of species from fragmented forest. The number of species in an area of once-continuous forest ( $S_{original}$ ) declines through the number ( $S_{now}$ ) at the time ( $t$ ) when a survey was conducted to the number that will eventually survive ( $S_{fragment}$ ). We can estimate  $S_{original}$  using  $S = cA^z$ , with  $z = 0.15$  and  $S_{fragment}$  using  $S = cA^z$  with  $z = 0.25$ . Because the decay is exponential, we can characterize it by a half-life, the time taken to lose 50% of the species.

1948, and anecdotal reports. Finally, we cataloged the historical bird specimens in most major museums, in particular the American Museum of Natural History (AMNH), the Academy of Natural Sciences of Philadelphia (ANSP), the Field Museum of Natural History (FMNH), the Museum of Comparative Zoology (MCZ), the National Museums of Kenya (NMK), and the U.S. National Museum (USNM). Our focus was on Kakamega, the only rainforest in Kenya, because its avifauna is well known and (especially) because it has four differently aged peripheral fragments for which we can reconstruct a deforestation history. These fragments are similarly sized (within one order of magnitude) and with one exception are isolated by similar distances (approximately 1 km).

Kakamega lies at 1400–1700 m in the Lake Victoria basin on the extreme eastern edge of the vast equatorial African rainforests. As such it has probably always been isolated to some degree. Anthropogenic effects have contributed a good deal to this isolation over the past few centuries. Kokwaro (1988: 473) noted that “The early explorers found the forests in widely scattered blocks, and these included the Kakamega-Nandi-Tindaret system or block . . . Parts had already been cleared by the advance of African shifting cultivators and by repeated firing of grasslands by pastoral tribes.” From this description, the Kakamega forest block had been fragmented from forests further west for many years.

At the time of British colonization of Kenya (in 1895), Kakamega was still contiguous with what are now the peripheral fragments of Yala, Ikuywa, Kisere, and Malava, and eastwards up the Nandi Escarpment to the Nandi Forests above 1800 m (Fig. 3). This forest block (excluding the high elevation Nandi Forests) would have covered approximately 25,000 ha. The fact that the area of forest originally gazetted (in 1933) was 23,777 ha (Kokwaro 1988) supports this estimate.

British colonization and the need to provide fuel for the wood-burning Mombasa-Kisumu railway (Kokwaro 1988) initiated a new wave of deforestation in western Kenya. In 1912 E. Heller wrote in *The Rainey African Expedition Journal of Edmund Heller* (USNM) that Kakamega “looks very solid but in reality it is everywhere broken by openings with shambas” (small farms). This period presumably also saw the isolation of Malava (“Kabras”), in which H. J. Allen Turner collected birds in 1917 (AMNH). A 1948 aerial photograph supports this, showing the southern edge of a forest halfway between Kakamega and Malava (Fig. 3a). When gazetted, Malava presumably covered at least 718 ha (Kokwaro 1988), and the aerial photographs show the forest covering 600 ha in 1965, but it has since been progressively eroded to its current size of 100 ha.

Kisere forest was probably isolated later because none of the collectors who hunted birds for V. G. L. van Someren and R. Meinertzhagen in the period 1912–1932 (AMNH, ANSP, FMNH, and NMK) mentioned visiting the site. It appears in 1948 aerial photographs at its present size (400 ha) and so has enjoyed some degree of protection since its isolation (Fig. 3a). Conservatively, we estimated that Kisere was isolated around 1933, when the forest was first gazetted. Most of the deforestation of Kakamega early this century thus seems to have occurred in the north.

Despite nominal forest protection from 1933 onward (Kenya Indigenous Forest Conservation Project 1994), the clearance of Kakamega has continued into recent years. By 1965, aerial photographs show that the forest was severed from South Nandi, resulting in the destruction of the old collecting localities of Kaimosi, Lerundo (“Nyarondo”; van Someren 1920), Bishago, and Silwa (AMNH, ANSP, FMNH, and NMK). It still covered approximately 15,000 ha and was contiguous with the Yala and Ikuywa forests

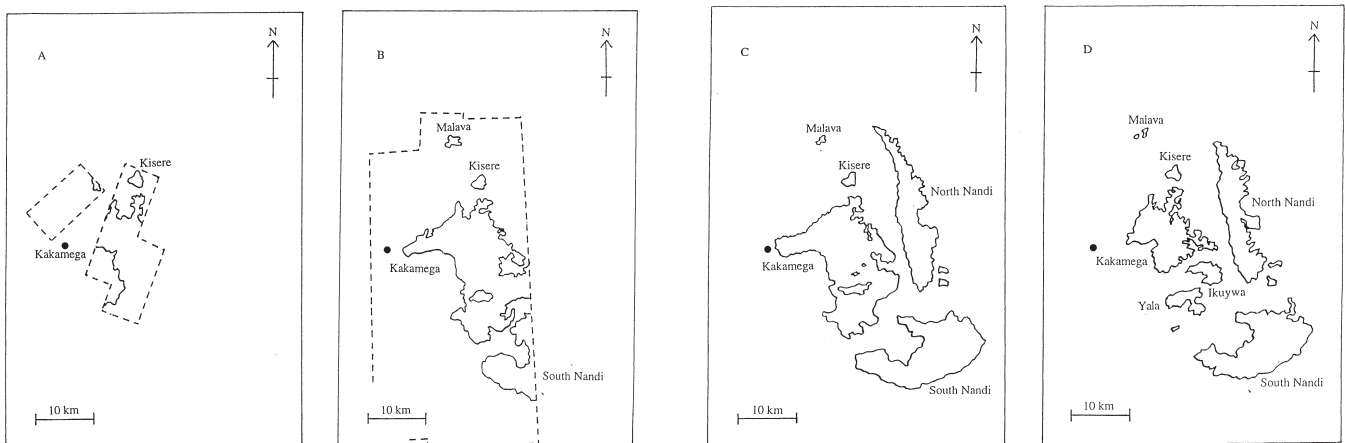


Figure 3. Sketch maps showing the extent of Kakamega rainforest in 1948 aerial photographs (a), 1965 aerial photographs (b), 1972 MSS satellite imagery (c), and 1989 TM satellite imagery (d). Dashed lines show the extent of aerial photographs, and black dots show the location of Kakamega town.

(Fig. 3b). Satellite imagery illustrates that by 1972 a broad east-west swathe had been cleared through the southern part of the forest, effectively isolating the Yala forest from the rest of Kakamega. A narrow connection to the Ikuywa forest (Fig. 3c) was retained.

By 1976 the southern fragments had suffered further loss, with Ikuywa separated from the main Kakamega forest and another portion of forest south of the Yala River cleared. A large area had also been deforested from the westernmost part of the forest next to Kakamega town. By 1979 the narrow connection between the Yala and Ikuywa forests was all but lost. Clearance slowed over the 1980s as forest protection was better enforced, but more areas were cleared south of the Yala River, as indicated by 1989 satellite imagery (Fig. 3d).

For 1989 areas of the Yala and Ikuywa forests were 1500 ha and 1450 ha, respectively. As of 1997, the main Kakamega forest covered 8600 ha. This closely matches the most recent published estimate of Kakamega's area in all sites (Table 1), of 10,100 ha of closed canopy and 2000 ha of other forest (Wass 1995). None of the forests were fragmented by a single event but rather by incremental deforestation. Nevertheless, forest cover data provide the best estimates of when each forest was separated from Kakamega.

We considered only "forest-specialist" species (Bennun et al. 1996), excluding those species that occur in open habitats. Our data came from a range of sources (Appendix). Most important was our own fieldwork, in which we combined extensive observation with mist-netting. Authors T.M.B., J.O.O., and other observers carried out extensive bird field surveys in February, April-May, and August-December 1996. We mist-netted in the peripheral fragments in April-May 1996 and in the main forest in April and September 1996. All nets were 3 m tall with 1.25-inch (3.17-cm) mesh. In each peripheral fragment (twice in Malava) and one main forest plot we ran 6000 meter-hours of mist-netting (200 m of net for 2 full days and 2 additional mornings); in eight additional main forest plots we ran 1600 meter-hours (200 m of net for 2 mornings).

We are confident that we detected all the species in the two small fragments (Kisere and Malava), but we are less

confident that our observations detected all species in the larger patches. Fortunately, three recent surveys (Stevenson 1991; Bennun & Waiyaki 1992; Bennun & Oyugi 1994) also covered these areas. There are problems with comparing and combining species lists from different surveys (Remsen 1994), but nevertheless these extra data effectively gave us full species lists for each of the sites.

Combined, these surveys showed 13 Kakamega species (Ripley & Bond 1971; Zimmerman 1972; Zimmerman et al. 1996) that have not been recorded in recent years. Of these, *Alcedo quadribachys* is a vagrant to Kenya with only one Kakamega record (Meadows et al. 1975). We found no proof of occurrence in Kakamega of either *Bostrychia olivacea* (Meinertzhagen 1937) or *Phoeniculus castaneiceps* (Jackson 1938). Excluding these three species leaves a total forest avifauna of 73 species.

Additionally, we could not trace recent records for 10 of the 73 species, and we found only a handful of recent records for a further 8 species. *Psittacus erithacus* was trapped to extinction for the cage-bird trade (Stevenson 1991). Three species that formerly reached their extreme eastern limits in Kakamega—*Raphidura sabini*, *Laniarius leucorhynchus*, and *Ploceus tricolor*—have been lost as the forest has been fragmented from the west. The remaining extinctions are of montane species (marked "M" in the Appendix), known from a number of historical specimens that presumably represented sink populations in Kakamega. Six of these have been lost as the forest was fragmented away from source populations in the high-elevation Nandi forests (1700–2100 m) to the east. Eight more species are now no more than rare visitors from the Nandi forests. To allow for the uncertainty in the status of these eight species, we gave  $S_{\text{now}}$  as a range (55–63; Table 2), and used the median value (59) in our calculations.

Using data from our field work and other published accounts (Appendix), we estimated the extent to which extinctions have occurred in Kakamega's isolated forest bird communities. To estimate the original numbers of species,  $S_{\text{original}}$ , in peripheral forests while they were still connected to Kakamega, we applied equation 1 with  $z = 0.15$ ,  $A_{\text{total}} = 25,000$ , and  $S_{\text{total}} = 73$ . To estimate final numbers of species following relaxation ( $S_{\text{fragment}}$ ), we applied equation 2 with  $z = 0.25$ . These values allowed us to use equation 3 to calculate relaxation indices ( $I$ ) and equation 4 to calculate half-lives for each fragment (Table 2).

## Results

The relaxation index ( $I$ ) indicates how close a fragment is to suffering so many extinctions that it reaches a new, lower equilibrium of species numbers. We plot  $I$  against the time ( $t$ ) since isolation of each fragment (Fig. 4). If species declines were all exponential with exactly the same half-lives, these points would fall along the same

**Table 1.** Geographic data for the surviving fragments of Kakamega rainforest, Kenya, 1989.

Fragment	Area (ha)	Elevation (m)	Distance (km)*	
			Main forest	Nearest patch
Malava	100	1500	9.4	9.0
Kisere	400	1500	1.6	1.6
Ikuywa	1450	1700	0.9	0.5
Yala	1500	1400	4.1	0.5
Kakamega	8600	1500–1600	—	0.9

\*Distance of fragment to main forest or nearest patch.

**Table 2. Bird extinctions from Kakamega forest fragments over time<sup>a</sup>**

Fragment	$A_{\text{fragment}}$ (ha)	$S_{\text{original}}$	$S_{\text{now}}^b$	$S_{\text{fragment}}$	I	t (years)	Half-life
Malava	100	32	19	18	0.05	101 (c.1895)	23
Kisere	400	39	(32) 31–32	26	0.45	63 (c.1933)	55
Ikuywa	1450	48	(44) 42–46	36	0.69	20 (1976)	38
Yala	1500	48	(44) 43–45	36	0.67	24 (1972)	42
Kakamega	8600	62	(59) 55–63	56	(0.49)	c.82 (1895–1933)	80

<sup>a</sup>The original area of forest ( $A_{\text{total}}$ ) is 25,000 ha, and the total species pool found in the original forest area ( $S_{\text{total}}$ ) is 73. We give the following data for each fragment: the current area of forest ( $A_{\text{fragment}}$ ); the number of species to be found in an area of this size were it part of a continuous forest ( $S_{\text{original}}$ ); the number of species in the fragment at the current time ( $S_{\text{now}}$ ); and the estimated future species number when all the extinctions have taken place ( $S_{\text{fragment}}$ ). The proportional loss of species provided a relaxation index (I) at the current number of years since fragmentation (t). The half-life of the declining avifaunas was calculated using equation 4.

<sup>b</sup>Where necessary, we show ranges of uncertainty in the values of  $S_{\text{now}}$  giving the median value in parentheses.

curve. To a rough approximation they do, and their calculated half-lives are all broadly similar at approximately <50 years (ranging from 23 to 80 years).

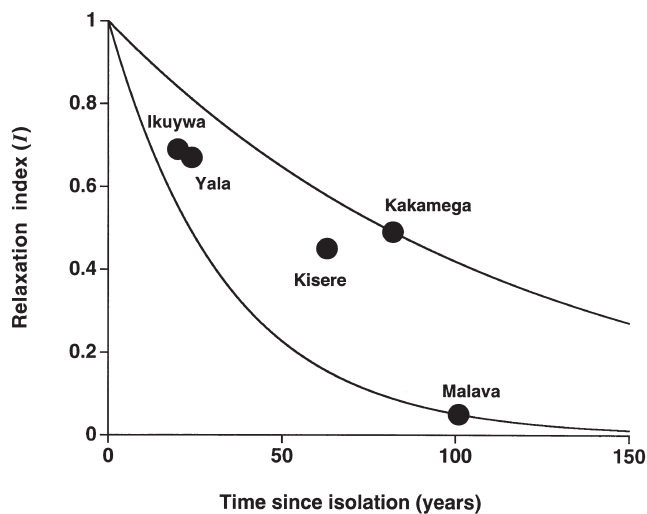
Various factors might explain the variation in half-lives of the fragments. Fragment size (Table 1) itself may be important because larger fragments should have smaller perimeter-to-area ratios and so be less affected by deleterious edge effects (Wilcove et al. 1986). This suggests that larger fragments should have longer half-lives than smaller fragments. Our data show this (Fig. 5;  $p = 0.05$ ): the main Kakamega forest, the largest fragment, had the longest half-life, and Malava Forest, the smallest fragment, had the shortest (Table 1).

Degree of spatial isolation should also be important (Table 1), with shorter distances between fragments allowing the “rescue-effect” (Brown & Kodric-Brown

1977) through continuing recolonization. Overall, the results are suggestive but not significant (Fig. 5). Malava forest, the most isolated fragment, had the shortest half-life (Table 2). Ikuywa forest was still occasionally visited by four montane species from the Nandi forests. In contrast, there are recent records of only two of these in the similar-sized but lower-elevation and more distant Yala forest (Appendix). The number of fragments is too small to separate the independent effects of fragment size and isolation.

What would be the consequences to the half-life estimates if we have not predicted  $S_{\text{original}}$  correctly? Reworking the results with a low  $z$  value of 0.05 to estimate new values for  $S_{\text{original}}$  had the effect of increasing them. This in turn meant that a higher proportion of species had been lost up to the current time. Consequently, this reduced the calculated half-lives describing extinctions from Kakamega’s forest fragments to approximately 25 years (across a range of 11–39 years).

Conversely, how sensitive are the values of  $S_{\text{fragment}}$  to the values of  $z$ ? If we were to use a  $z$  value as high as 0.35 to estimate how many species will survive in each of the Kakamega fragments after relaxation, then the calculation would show that more species would be lost eventually. A smaller proportion of these would have already been lost as the the calculated half-lives would double to approximately 100 years (72–182 years). If we were to use a high  $z$  value (0.35) to estimate  $S_{\text{fragment}}$  and a low  $z$  value (0.05) to estimate  $S_{\text{original}}$ , the calculated half-lives return to around 50 years (18–74 years). A half-life of 50 years emerged as a plausible value, with extremes of twice and half that duration.



**Figure 4.** Proportion of species expected to remain, I, against their times since isolation, t. The curves indicate exponential decay from the fragments with the shortest (Malava, lower line) and longest (Kakamega, upper line) half-lives.

## Discussion

Bird communities in small fragments of Afrotropical forest take less than a century and maybe as little as a quarter-century to relax halfway toward a new, lower equilibrium number of species. Should one expect such a

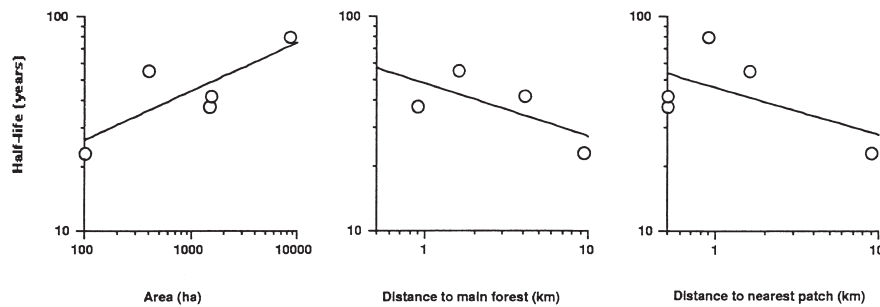


Figure 5. Relationships between half-lives and geography of Kakamega's forest fragments. The half-life of the exponential loss of species from fragmented forest increases with forest area and decreases with isolation. Power functions describes these relationships.

half-life? There are far fewer data to answer this question than one might expect given the interest ecologists have in fragmentation.

Numerous studies show that small fragments lack many species found in large fragments (Turner 1996). Only rarely, however, do studies define the length of time that the fragment has been isolated (Laurence et al. 1997). Even then, some studies cannot provide precise dates (e.g., Leck 1979) or numbers of species (e.g., E. Ruelas Inzunza, unpublished data). A few studies do provide dated historical and contemporary information on bird communities in fragmented tropical forests (Diamond et al. 1987; Karr 1994; Kattan et al. 1994; Aleixo & Vielliard 1995; Christiansen & Pitter 1997; Corlett & Turner 1997; L.M. Renjifo, unpublished data). Future resurveys of these sites could provide a third point in time along the relaxation curve (Fig. 4) and therefore test our predictions.

The experimental studies at Manaus (Bierregaard & Stouffer 1997) and Lago Gurí (Terborgh et al. 1997) are broadly consistent with half-lives of a few decades. The Manaus project has seen the loss of species following isolation nearly two decades ago. At Lago Gurí, islands formed by flooding a reservoir two decades ago contain fewer species than are found in forests on the nearby mainland. To our knowledge, neither study has attempted quantitative estimates of the rate of species loss.

There are only two previous estimates of half-lives. They are for tropical forest birds on islands in the southwestern Pacific (Diamond 1972) and the Caribbean (Terborgh 1974). These islands have been isolated since sea-level rise 10,000 years ago. Their estimated half-lives are 1000–10,000 years, two orders of magnitude longer than those we found. This could be a result of several factors. All of the islands considered in these studies are considerably larger than the Kakamega fragments: 13,000–780,000 ha for the southwestern Pacific and 600–482,000 ha for the Caribbean. Both Diamond (1972) and this study (Fig. 5) show that relaxation rates are scale-dependent.

Alternatively, Boecklen and Simberloff (1986) suggest that Diamond (1972) and Terborgh (1974) overestimated Pleistocene history (i.e.,  $t$ ) or the initial number of species (i.e.,  $S_{\text{original}}$ ). If so, the correct half-lives would be shorter. Finally, mainland habitat islands such

as Kakamega may be subject to considerably more serious external effects (Janzen 1986)—fire, storms, predation, parasitism—than are oceanic islands, which may shorten half-lives on the mainland. Direct persecution by humans may affect large species in particular (Woodroffe & Ginsberg 1998).

An extension of our results asks how half-lives describing extinction following habitat fragmentation scale to other taxa in other habitats. For mammals in isolated Tanzanian parks (Newmark 1996) and birds in fragments of Californian chaparral (Bolger et al. 1991), many extinctions have occurred within a century of habitat loss. More directly, Leach and Givnish (1996) found a half-life of 50–100 years for plant species in 54 Wisconsin prairie remnants 0.2–6 ha in area. This half-life is similar to the one we report, although presumably this similarity is coincidental. Half-lives must depend on the generation time and dispersal ability of the taxa in question in relation to the size of the fragment under consideration.

Overall, our results provide both encouragement and warning. On the positive side, we quantify Turner and Corlett's (1996) suggestion that tropical forest fragments "can retain a relatively large proportion of their biodiversity decades after isolation." For birds, at least, a fragmented community will have relaxed about 50% of the way toward its future equilibrium after 25–100 years. This shows that managers do have a small breathing space in which to carry out conservation actions, for example, protection from disturbance, reforestation, or active management for particularly threatened species. It also gives some indication of where one should target conservation efforts. Other things being equal, for example, the species of a recently isolated forest fragment will be in much greater danger than those surviving in a century-old fragment, which has already lost many species to approach a lower equilibrium (Balmford 1996).

On the negative side, we show clearly how fast biodiversity is being lost from the remnants that increasingly are all that survive of the world's tropical forests. On local scales, substantial numbers of species are certainly lost from tropical forest patches in their first decade after fragmentation (Fig. 4). Further, we can apply our results globally because the majority (65%) of the world's

1111 threatened bird species are found in forests (Collar et al. 1994). We can therefore predict that 50% of these—approaching 500 species—will be extinct in approximately 50 years (Pimm & Brooks, 1999). Simple extrapolation of this result further supports the already considerable evidence that current extinction rates are at least 1000 times higher than the background rate (Pimm et al. 1995). In short, tropical forest fragmentation is causing extinctions both locally and globally at unprecedented rates.

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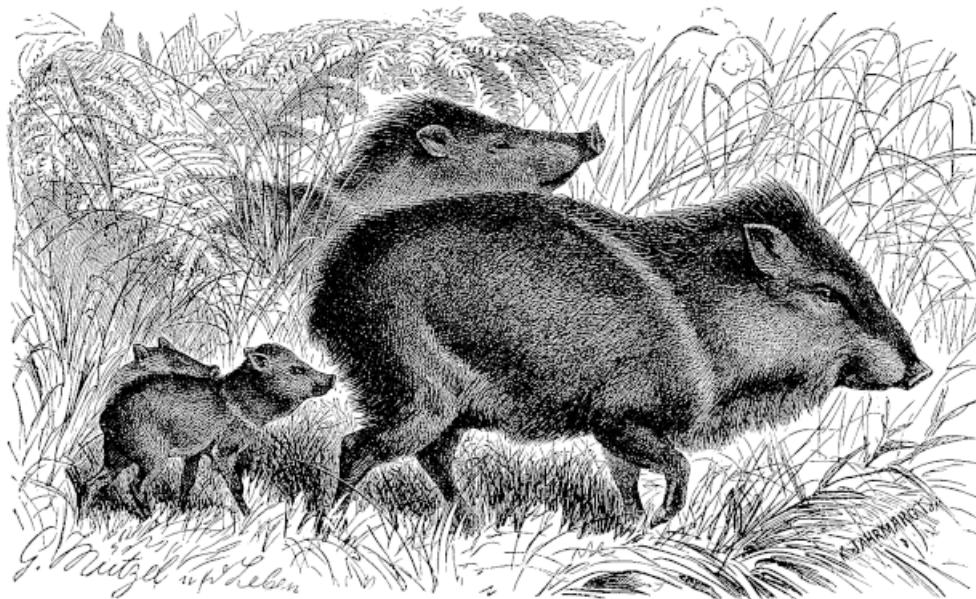
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## Appendix

Forest-specialist species (Bennun et al. 1996) surviving in Kakamega forest and its peripheral fragments.<sup>a</sup>

Species	Kakamega	Yala	Ikuywa	Kisere	Malava
<i>Bostrychia olivacea</i> M					
extinct if ever occurred (Zimmerman et al. 1996)					
<i>Buteo oreophilus</i> M	4	3	8		
<i>Stephanoaetus coronatus</i>	2	2	2		
<i>Sarothura elegans</i>	2	3	2		2
<i>Columba delagorguei</i> M	4				
<i>Columba arquatrix</i> M					
extinct?, last records 1973–1975 (Mann 1985)					
<i>Aplopelia larvata</i> M	4			1	
<i>Psittacus erithacus</i>					
extinct, although non-breeding stragglers still occur (Jackson 1996)					
<i>Tauraco schuetti</i>	2	2	5		
<i>Tauraco bartlaubi</i> M					
extinct?, last records 1980 (Angwin 1980)					
<i>Glaucidium tephronotum</i>	1	2			
<i>Raphidura sabini</i>					
extinct, one post-1990 record (L.A. Bennun, personal communication)					
<i>Apaloderma vittatum</i>	3	3	2		
<i>Alcedo quadribrachys</i>					
vagrant, one bird Nov. 1974–Jan. 1975 (Zimmerman et al. 1996)					
<i>Merops muelleri</i>	1	2	2	2	
<i>Phoeniculus bollei</i>	2	2	2	2	2
<i>Phoeniculus castaneiceps</i>					
extinct if ever occurred (Zimmerman et al. 1996)					
<i>Buccanodon duchaillui</i>	2	2	2	1	2
<i>Indicator conirostris</i>	4				
<i>Indicator exilis</i>	2	1			
<i>Prodotiscus insignis</i>	4		2		
<i>Campetbera tullbergi</i> M					
extinct?, last record 1965 (USNM #519440)					
<i>Dendropicus xantholophus</i>	5	3			
<i>Smithornis capensis</i>	1	2	2	2	
<i>Andropadus curvirostris</i>	1	1	1	1	1
<i>Andropadus gracilis</i>	1	2			
<i>Andropadus ansorgei</i>	1	2	1	1	
<i>Andropadus gracilirostris</i>	2	2	2	2	2
<i>Andropadus masukuensis</i>	1	2	1		
<i>Phyllastrephus hypochloris</i>	1	1		1	
<i>Phyllastrephus cabanisi</i>	1	1	1	1	1
<i>Baeopogon indicator</i>	2	2	2		
<i>Bleda syndactyla</i>	1	1	1	1	1
<i>Pseudoalcippe abyssinica</i> M	9		8		
<i>Kakamega poliothorax</i>	1		6		
<i>Illadopsis fulvescens</i>	1	1	2	1	1
<i>Illadopsis pyrrhoptera</i>	1		1	2	1
<i>Illadopsis rufipennis</i>	1	1	1	1	
<i>Illadopsis albipectus</i>	1	1	1	1	1
<i>Sheppardia aequartorialis</i>	1	1	1	1	1
<i>Sheppardia polioptera</i>	3		1	2	1
<i>Alethe poliocephala</i>	1	1	1	1	1
<i>Neocossyphus poensis</i>	1	1	2	2	
<i>Muscicapa lendu</i>	1		5		
<i>Phylloscopus budongoensis</i>	1	1	2	1	2
<i>Bathmocercus rufus</i>	1	1	1	1	2
<i>Camaroptera chloronota</i>	1	1	1	1	
<i>Apalis rufogularis</i>	2	3	2	2	
<i>Apalis cinerea</i>	4	3			
<i>Apalis jacksoni</i>	6				
<i>Sylvietta leucophrys</i> M	5		1		
<i>Eremomela turneri</i>	2	2	2	2	2

continued

## Appendix (continued)

Species	Kakamega	Yala	Ikuywa	Kisere	Malava
<i>Parus funereus</i>	2	2	2	2	
<i>Trochocercus albonotatus</i> M extinct?, last records from 1973–1975 (Mann 1985)					
<i>Terpsiphone rufiventer</i>	4		8		
<i>Bias flammulatus</i>	2	2			
<i>Dyaphorophoria castanea</i>	1	1	1	2	
<i>Dyaphorophoria jamesoni</i>	1	1	1	1	1
<i>Dyaphorophoria concreta</i>	1	2			
<i>Laniarius leucorhynchus</i> extinct, only record 1931 (FMNH #200868)					
<i>Dryoscopus angolensis</i>	2	2	2	2	
<i>Campephaga petiti</i>	2	2	2		
<i>Campephaga quiscalina</i>	2		2	2	
<i>Coracina caesia</i> M	3	3	2		
<i>Oriolus percivali</i> M extinct?, last record 1965 (USNM #521734)					
<i>Poeyoptera stublmanni</i>	2	2	2		
<i>Oncobognathus walleri</i> M	4				
<i>Cinnyricinclus scharpii</i> M extinct?, last records 1973–1975 (Mann 1985)					
<i>Anthreptes rectirostris</i>	2	4			
<i>Nectarinia olivacea</i>	1	1	1	1	1
<i>Ploceus melanogaster</i>	2		1	1	2
<i>Ploceus tricolor</i> extinct, last records 1965 (Zimmerman 1972)					
<i>Ploceus insignis</i>	2		2	2	
<i>Malimbus rubricollis</i>	2	2	2		
<i>Mandingoa nitidula</i>	2				
<i>Serinus burtoni</i> M	7				
Total species <sup>b</sup>	55–63(59)	43–45(44)	42–47(45)	31–32(32)	19

<sup>a</sup>Documentation is as follows: (1) mist-netted during our fieldwork; (2) observed during our fieldwork; (3) Bennun and Oyugi (1994); (4) Bennun and Waiyaki (1992); (5) Stevenson (1991); (6) D. A. Turner, personal communication; (7) L. A. Bennun, personal communication; (8) J. Hornbuckle and R. A. Frost, unpublished birdwatching report; (9) J. E. Potts and S. J. Marsden, unpublished birdwatching report. We also refer to several museum specimens and general publications. We are preparing full documentation of the current conservation status of the forest bird species of Kakamega forest for publication elsewhere. Species marked with an M are typical of Kenya's montane forests (one of which probably never occurred in Kakamega, six of which did once but are now extinct in the forest, and the remaining eight of which are now probably only rare visitors).

<sup>b</sup>Numbers of species exclude local extinctions and *Bostrychia olivacea*, *Phoeniculus castaneiceps*, and *Alcedo quadribrachys* which were probably never part of the resident Kakamega avifauna. Ranges indicate uncertainty over the status of eight species that are now only rare visitors from the montane Nandi forests. Median value in parentheses.

