PRIMATE SURVIVAL IN COMMUNITY-OWNED FOREST FRAGMENTS:

Are Metapopulation Models Useful Amidst Intensive Use?

Colin A. Chapman, Michael J. Lawes, Lisa Naughton-Treves, and Thomas Gillespie*

1. INTRODUCTION

Human modification of ecosystems is threatening biodiversity on a global scale (Cowlishaw, 1999; Cowlishaw and Dunbar, 2000; Chapman and Peres, 2001). A recent Food and Agriculture Organization report (FAO, 1999) indicates that tropical countries are losing 127,300 km^2 of forest annually, and this does not consider the vast area being selectively logged (approximately 55,000 km^2; FAO, 1990). The extent of tropical forests burning each year is highly variable and difficult to measure precisely (FAO, 1999; Nepstad et al., 1999), however, the forests of Southeast Asia (Kinnaird and O'Brien, 1999) and the Brazilian Amazon (Nepstad et al., 1999) are especially impacted by the combination of droughts from El Niño and burning for agriculture (FAO, 1999). In 1997 and 1998 an area of 2 million ha of forest burned in Brazil and 4 million ha burned in Indonesia (FAO, 1999).

These modifications to tropical forests do not just result in the forest being uniformly reduced in size, they also result in forest being fragmented. To understand the conservation value of these fragments is critical, because they may represent opportunities to make important conservation gains. The reason fragments become important for conservation is related to the fact that, today, less than 5% of tropical forests are legally protected from human exploitation, and many of these legally protected areas are subjected to illegal exploitation (Redford, 1992; Oates, 1996). Furthermore, many tropical species are locally endemic or are rare and patchily

* Colin A. Chapman, Department of Zoology, University of Florida, Gainesville, Florida, 32611 and Wildlife Conservation Society, Bronx, New York, 10460. Michael J. Lawes, Forest Biodiversity Programme, School of Botany and Zoology, University of Natal, Bag X01, Scottsville, 3209, South Africa. Lisa Naughton-Treves, Department of Geography, University of Wisconsin, Madison, Madison, Wisconsin, 53706 and Center for Applied Biodiversity Science, Conservation International, Washington, DC, 20036. Thomas Gillespie, Department of Zoology, University of Florida, Gainesville, Florida, 32611. Correspondence to C. A. Chapman (email: cachapman@zoo.ufl.edu).

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distributed (Struhsaker, 1975; Richards, 1996). Such restricted distributions predispose many tropical forest species to an increased risk of extinction when habitats are modified (Terborgh, 1992), because national parks and reserves, even if effectively protected, will fail to conserve species whose ranges do not fall within a protected area. As a result, conservation of many tropical forest species will depend on the capacity of fragmented forests to support their populations. Primates are valuable species to study the effects of fragmentation because they are relatively easy to census, and there is often a large body of information on their behavior from intact forests. Furthermore, because many species are locally endemic and endangered or threatened, it is critical to formulate informed management plans.

Ecological research over the last decade reveals that conserving animals in forest fragments is difficult given the unpredictable and complex interactions between species experiencing rapid habitat change (Laurance and Bierregaard, 1997). With respect to primates, this difficulty arises from three sources. First, a number of simple logical predictions made by some of the first researchers studying primates in forest fragments have not proven to be general. For example, home range size is frequently cited as influencing a species ability to survive in a fragment (Lovejoy et al., 1986; Estrada and Coates-Estrada, 1996). However, Onderdonk and Chapman (2000), found no relationship between home range size and the ability to live in fragments for a community of primates in Western Uganda. Similarly, it has been suggested that a highly frugivorous diet may limit the ability of a species to live in fragments (Lovejoy et al., 1986; Estrada and Coates-Estrada, 1996). However, Tutin et al. (1997) found that several frugivorous species were at higher or similar densities in forest fragments than in the intact forest of Lopé Reserve, Gabon (Tutin, 1999; Onderdonk and Chapman, 2000). The complexity of the issue is illustrated by redtail monkeys frequently moving between forest fragments near Kibale, using available forest corridors and crossing agricultural areas; whereas, blue monkeys, which have a similar diet and social organization, do not use these fragments or corridors (Chapman and Onderdonk, 1998; Onderdonk and Chapman, 2000). In contrast, blue monkeys near Budongo Forest Reserve, Uganda, often reside in fragments and travel through agricultural land (Fairgrieve, 1995).

Secondly, studies of fragments and their primate populations often involve attempts to understand dynamic systems. Typically, studies are conducted in areas where the long-term history of the fragments is not well known. One does not know if a study population in the fragment is at equilibrium or not. Many years may pass after isolation before a population will respond numerically to fragmentation. For example, Struhsaker (1976) documented that it was nearly 10 years after the loss of approximately 90% of a major food resource that a statistically significant decline in vervet monkeys (*Chlorocebus aethiops*) at Amboseli, Kenya, could be detected. Furthermore, the human use of fragments and resulting ecological impacts are too often ignored. Most fragments are not protected; they are on private land and are used by local landowners. Thus, fragments change structure and composition as landowners use the forest for grazing or to extract timber or fuelwood or allow fallow land to regenerate. This fact has not been fully appreciated, probably because a number of previous studies have been conducted in forest fragments that are protected (i.e., they are within a protective reserve; Lovejoy et al., 1986; Tutin et al., 1997; Tutin 1999). While these studies in protected reserves have provided us with many insights, they are not typical of most fragments, and they may have biased our perception of the value of forest fragments to primates.

Third, although the theoretical effects of habitat isolation and fragment size are well known (Hanski, 1994; Hanski and Gilpin, 1997), their effects on individual species are rarely studied in detail (Harrison et al., 1988; Thomas et al., 1992). Where they are, it is generally acknowledged that fragmentation of once continuous habitat has had a detrimental effect on species' persistence (Laurance and Bierregaard, 1997), and there is hope that species may persist in metapopulations. The dynamics and persistence of such metapopulations are governed by the interaction between the life history of species, which determines the rates of local extinction and colonization, and landscape properties (e.g., area of the fragment, distance to other fragments, Hanski, 1994). However, robust and predictive metapopulation models of a species persistence in fragmented forests demand data from a large number of fragments (>40 fragments, Hanski and Gilpin, 1997; Lawes et al., 2000). The difficulties of surveying a large number of fragments frequently limits data to presence-absence records that provide limited information on life-history constraints (e.g., density, diet, fecundity) or species persistence. These difficulties do not easily reveal the processes responsible for observed patterns of persistence and distribution. As a result, insights are difficult to gain from the theoretical models that can be accurately applied to management objectives.

The objectives of this study were to (1) document the changes in forest structure of a series of forest fragments outside of Kibale National Park, Uganda, over a 5-year period, (2) describe the persistence of primates in those fragments over that period, (3) quantify changes in the size and structure of black-and-white colobus (*Colobus guereza*) populations, and 4) consider the value of metapopulation models, particularly incidence-function models, to the management of this community-owned forest fragment system. The area in which these fragments are located is a matrix of small-scale agriculture, grazing land, and tea plantations. Local residents are using all fragments for multiple purposes, including fuelwood collection and charcoal manufacture. Although we have a relatively small data set relative to what is needed for metapopulation modeling, we use a simple incidence function metapopulation model to investigate patterns of primate fragment occupancy. We also incorporate the life-histories of the primate species and the landscape properties in our analyses.

2. METHODS

2.1. Study Site

The primates in 20 forest fragments were censused from May to August 1995 (Onderdonk and Chapman, 2000), and 19 were recensused in May to August 2000. These forest fragments are neighboring Kibale National Park, Uganda (766 km^2), located in western Uganda (0 13' - 0 41' N and 30 19' - 30 32' E) near the foothills of the Rwenzori Mountains. Kibale is a mid-altitude moist evergreen forest that receives approximately 1,750 mm (1990 to 1999) that falls primarily in two rainy seasons (Chapman et al., 1997; Struhsaker, 1997; Chapman and Lambert, 2000). Before clearing for agriculture, there was likely continuous forest throughout the study region and it was directly connected to what is now Kibale forest. The forest in the fragments was probably similar to the forest within the national park, but it has been largely deforested and is now dominated by smallholder agriculture.

The forests and wildlife of western Uganda have long been influenced by human activities, but these activities have dramatically intensified over the past 50 years (Howard, 1991, Naughton-Treves, 1999). Pollen records suggest that forest clearing began in Uganda at least 1,000 years ago with the introduction of agriculture and iron making (Hamilton, 1974, 1984). Until the 20th century, the forests of western Uganda were sparsely settled by Bakonjo and Baamba hunter-gatherers (Taylor, 1962; Steinhart, 1971). War and epidemics likely caused forests to expand at the end of the 19th century (Osmaston, 1959; Paterson, 1991). Shortly thereafter, Batoro herders and agriculturalists arrived in the region from the north, displaced the Bakonjo and Baamba, and began a lengthy period of deforestation. By the end of the 20th century, nearly all forest outside of officially protected areas has been converted to farms, grazing areas, or tea plantations (Naughton-Treves, 1997). Only small pockets of forest remain in areas unsuitable for agriculture. Thus, the forest fragments that we studied were either forested areas associated with swampy valley bottoms or on the steep forested rims of crater lakes (Table 1). While the precise timing of isolation of these forest remnants is not known, local elders describe them as 'ancestral forests' (Naughton-Treves, unpublished data). Aerial photographs taken in 1959 indicate that most fragments have been isolated from Kibale at least since that time, although many have decreased in size. Oral histories suggest that they have been present for decades.

Human population surrounding Kibale has increased seven-fold since 1920, surpassing 272 individuals per km^2 at Kibale's western edge (versus 92 per km^2 for the District; NEMA, 1997). Population growth rate varies among parishes, but is typically between 3% and 4%. (In the parishes with the majority of the fragments growth rate

Table 1. Characteristics of forest fragments outside of Kibale National Park, Uganda[a].

Fragment	Area (ha)	Fragment Type	Distance to Kibale (km)	Nearest Fragment (m)	Redtail	Red Colobus	B&W Colobus	Chimp	Forest Status
Rutoma #3	0.8	HS	2.2	100	1/0	0/0	0/0	1/0	Deforested
Dry Lake	1.2	HS	6.1	153	1/0	0/0	1/0	0/0	Deforested
Rutoma #1	1.2	HS	2.4	80	1/1	0/1	1/1	1/0	Remaining
Kiko #4	1.2	VB	1.1	70	0/0	1/1	1/1	1/0	Remaining
Durama	1.4	HS	1.1	60	1/0	0/0	0/0	0/0	Deforested
Kiko #3	1.7	VB	1.1	70	1/0	1/1	1/1	0/0	Remaining
Rutoma #4	2.0	HS	2.1	80	1/0	0/0	1/0	0/0	Deforested
Lake Nyanswiga	2.2	CL	6.0	155	1/1	0/0	1/1	1/1	Remaining
Kyaibombo	2.3	VB	1.1	162	1/0	0/0	1/0	0/0	Deforested
Ruihamba	2.4	VB	4.1	300	0/1	0/1	1/1	0/1	Remaining
Nkuruba - Fish Pond	2.8	VB	3.7	70	1/1	1/1	1/1	1/1	Remaining
Lake Nyaherya	4.6	CL	6.1	300	1/1	0/1	1/1	0/1	Remaining
Rutoma #2	4.9	HS	3.0	150	1/0	0/1	1/1	1/0	Remaining
Rusenyi	4.9	VB	1.1	50	1/1	0/1	1/1	0/0	Remaining
Kiko #2	5.0	VB	1.8	125	1/0	1/1	1/1	0/0	Remaining
Kiko #1	6.2	VB	2.0	50	1/0	1/1	1/1	0/0	Remaining
Nkuruba Lake	6.4	CL	3.6	70	1/1	0/1	1/1	1/1	Remaining
CK's Durama	8.7	VB/HS	0.2	150	1/0	1/1	1/1	1/0	Remaining
Lake Mwamba	28.7	CL	7.2	100	1/?	0/0	0/0	0/0	Remaining

[a] The presence (1) and absence (0) of each species in 1995 and 2000 are indicated (95/00). Forest Status is labeled as deforested when it is viewed by the researchers to have insufficient trees remaining to support resident primate populations and no residents were seen in the 2000 survey. If a solitary individual was in a fragment, it was not assumed that the fragment could support the species (HS = Hillside, VB = Valley Bottom, CL = Crater Lake).

averages 3.87%; NEMA, 1997.) Batoro farmers remain the dominant local ethnic group in the area (~52% of population). However, waves of other immigrants into the area (e.g., Bakiga) have intensified the demand for agricultural land and forest products (NEMA, 1997; MFEP, 1992).

Of Kibale's 12 primate species (chimpanzees–*Pan troglodytes*, gray-cheeked mangabey–*Lophocebus albigena*, red colobus–*Procolobus badius*, black-and-white colobus–*Colobus guereza*, red-tailed monkeys–*Cercopithecus ascanius*, blue monkeys–*C. mitis*, l'hoest's monkey–*C. lhoesti*, vervets–*Chlorocebus aethiops*, olive baboon–*Papio anubis*, potto–*Perodictus potto*, Matschie's bush babies–*Galago matshiei*, and Thomas's bush babies–*Galagoides thomasi*), only six have been recorded in the fragments (red-tailed monkeys, chimpanzees, baboons, red colobus, black-and-white colobus, and vervets; fragments have not been sampled for the three nocturnal primates).

2.2. Surveying Primate Fragment Occupancy

In 1995, forest fragments were selected if they had a fairly clearly defined boundary, were isolated from other fragments or tracts of forest by ≥50 m, and were small enough to count all black-and-white colobus groups. Twenty fragments were visited in the first survey. One large fragment was surveyed in 1995, but was not resurveyed. In the first survey the following parameters were measured in each fragment: primate species present, black-and-white colobus group size and composition, tree species richness, area of the fragment, and distance to the nearest fragment (see Onderdonk and Chapman, 2000 for details of these methods). We determined which primate species were present by observations made over a 2- to 4-day period. Ideally, species abundance rather than presence-absence would be used as an index of success in a fragment, but these data were only possible to obtain for the black-and-white colobus. For each group of black-and-white colobus encountered we determined size and composition (age/sex classes follow Oates, 1974). To obtain reliable estimates of group counts an observer would often stay with a group for up to a day and wait for members to make a coordinated movement crossing an opening. Since many of the fragments were on the slopes of the crater lakes, we were often able to get above the group. In such instances, animals were highly visible.

In the survey conducted in 2000, the same parameters were measured, with the exception of fragment size and distance to the next fragment, although changes in the condition of the fragments were noted. In addition, in the second survey the composition of red colobus groups was determined. Detailed descriptions of how the fragments were being used by the local people were also recorded. From long-term research at one fragment (Lake Nkuruba, Chapman et al., 1998), we know that redtail monkeys and chimpanzees frequently move among fragments (i.e., they use multiple fragments in a week). In contrast, the colobines are much more site tenacious and rarely move among fragments (i.e., to colonize a new fragment). As a result, when contrasting presence-absence data between time periods, we focus on colobines.

2.3. Environmental Factors and Forest Use by Local Landowners

The forest fragments we studied provide multiple resources to local citizens, including medicinal plants, foodstuffs, fodder, building materials, and, most importantly, fuelwood (Table 2). Over 98% of residents neighboring Kibale rely exclusively on

Table 2. Patterns of land use of 16 of the 19 fragments used to assess the long-term viability of primate populations in forest fragments near Kibale National Park, Uganda[a].

Forest Fragment	Area (ha)	Households	Ethnicity (Dominant)	Tenure	Brew Beer	Distill Gin	Charcoal	Cattle/ Goats	Woodlot
Rutoma I	1.2	8	Mixed[b]	V	0	25	0	0	13
Kiko #4	1.2	5	Mixed (K)	T	0	0	0	0	100
Durama	1.4	4	Mixed (T)	V	50	0	0	0	75
Kiko #3	1.7	3	Mixed[b]	T	0	0	0	0	33
Rutoma IV	2.0	8	Mixed (T)	V	25	0	13	38	38
Lake Nyanswiga	2.2	4	Mixed (T)	V	0	0	50	25	25
Kyaibombo	2.3	7	Toro	C	29	29	14	43	86
Rwaihamba	2.4	8	Mixed (T)	V	25	38	0	50	88
Nkuruba - FishPond	2.8	2	Other	C	0	0	0	50	100
Lake Nyaherya	4.6	8	Mixed (T)	V	0	0	63	13	13
Rusenyi	4.9	11	Toro	V	9	9	27	0	27
Kiko #2	5.0	6	Mixed (K)	T	0	0	50	0	50
Kiko #1	6.2	9	Mixed (K)	T	0	0	0	11	44
Nkaruba Lake	6.4	2	Other	C	0	0	0	0	50
Ck'sDurama	8.7	16	Mixed (K)	V	6	31	0	12.5	50

[a] Ethnicity includes Batoro (T), Bakiga (K), and Other (Mzungu, Munyankole, Catholic Church, etc.), mixed indicates that households from a number of ethnic groups were using the fragment. For the other parameters reported we indicate the percentage of the households that were engaged in the indicated activity (e.g., brewing beer). Land tenure types – V = customary claim by village, T = property of tea company, C = property of Catholic Church. [b] no dominant ethnicity.

fuelwood or charcoal for energy; one of the highest levels in the world (Bradley, 1991; Government of Uganda, 1992). Rapid population growth, expanded commercial charcoal and brick production, industrial fuelwood demands, and technological change are fundamentally altering the relationship between forests and forest users. Furthermore, the demand for forest products has intensified in a context of insecure property rights, resulting in rapid deforestation.

The land and tree tenure arrangements governing local access to resources in these forest fragments are complex and rooted in customary systems. Traditionally, clans governed land use and allocated plots to individual members who then carefully demarcate their property by planting living fences or clearing fields. This system has largely persisted, despite the nationalization of all land in Uganda in 1975 (Place and Otsuka, 2000), and is the de facto tenure system for a majority of the fragments we studied. Seven of the forest fragments are formally held under semi-permanent leaseholds by the Catholic Church or tea company, but both the Church and the tea company permit local residents to use the forests according to customary systems. Traditionally, individuals managing plots of forest allowed kin to freely harvest firewood, drinking water, and medicinals from their property, although certain species, hardwoods in particular, required special permission to harvest (Kaipiriri, 1997). Many villagers today complain that controlling access to their forests has become difficult, given increasing scarcity and value of forest resources. As is typical of much of the tropics, they often resort to deforestation as a means of securing land ownership (Sjaastad and Bromley, 1997). Others are bribed or coerced by charcoal manufacturers to allow them to produce charcoal in their forest.

To better understand forest use by local citizens and its potential impact on primate survival, we collected detailed data on how fragments were being used by the local people, as well as general socioeconomic parameters for each fragment. For example, for 16 of the 19 fragments, we determined the number of households that owned land directly adjacent to the forest. Fragments are considered to be property of these households and thus the number of households should represent an index of pressure on the fragment. We also noted the ethnicity of households (Bakiga immigrants are thought to use forests more intensively than Batoro residents, Kaipiriri, 1997) and whether they had eucalyptus woodlots on their land. Woodlots may take pressure off fragments, because landowners would have access to alternative fuelwood sources. Alternatively, plantations may indicate that fuelwood resources in the fragments are being depleted and farmers are now planting trees on their own land to have access to fuel in the future. Finally, for each household we interviewed residents and determined if they were using fuelwood from the fragment to brew beer, distill gin, and/or produce charcoal. We also determined if each household had goats or cattle since these animals are often allowed to graze in fragments.

2.4. The Incidence-Function Model

A population that consists of several subpopulations linked together by immigration and emigration is regarded as a metapopulation. The fraction of suitable habitat fragments occupied at any given time (incidence) represents a balance of the rate at which subpopulations go extinct in occupied fragments and the rate of colonization of empty fragments. However, the measurement of colonization and extinction rates is very time-consuming and thus the practical application of metapopulation models can be difficult. Hanski (1994) has argued that incidence functions, based on relatively easily collected presence-absence data from a large number of fragments, can provide relative or absolute rates of extinction and colonization at low cost.

Here we used an incidence function to model the presence or absence of a primate species in any given fragment. Incidence functions are discrete-time stochastic fragment models and a metapopulation-level extension of a first-order Markov chain model for an individual fragment (Hanski, 1994). However, to generate state transition probabilities from a species-incidence curve derived from one survey, we assume that occupancy of the system at the time of the survey is at equilibrium (Hanski, 1994; Thomas, 1994). As a means of determining whether or not primate metapopulations are indeed in a steady-state, we compare species fragment occupancy models between two time periods. The difference in fragment occupancy between time periods enables a prediction probability of future persistence and consequences of habitat loss to a suite of forest primates.

Hanski (1994) showed that if fragment i is currently empty, it has the probability, C_i, of becoming recolonized in unit time, and if fragment i is currently occupied, it has a constant probability, E_i, of becoming empty (local extinction). This elementary model describes the incidence of a species in fragment i as the stationary probability of fragment occupancy (J_i):

$$J_i = C_i / (C_i + E_i) \qquad (1)$$

To account for the generally observed trends of increasing occupancy with increasing area and decreasing isolation, an incidence function model based on a metapopulation consisting of a 'mainland' (whose population is invulnerable to extinction) with small forest fragments around it (i.e., mainland-island incidence-function model) requires the following assumptions (Hanski 1994; Lawes et al., 2000): 1) the colonization probability, C_i, is a negative exponential function of distance from the mainland; 2) the relatively week dependence of colonization on fragment area, A_i, is ignored; and 3) the extinction probability, E_i, strongly depends on fragment area but not on isolation. Hanski (1994) provides an elementary mainland-island incidence-function model that combines these assumptions into one function. The colonization probability model is given by

$$C_i = e^{-\beta D_i} \tag{2}$$

where D_i is the distance of the ith fragment from the mainland, in this case Kibale National Park, and β is a constant. The extinction probability model is

$$E_i = \frac{c}{A_i^x}, \tag{3}$$

where A_i is the area and c and x are constants. Substituting (Eq. 2) and (Eq. 3) into (Eq. 1) yields the incidence function for the mainland-island metapopulation model as

$$J_i = \frac{1}{1 + \dfrac{ce^{\beta D_i}}{A_i^x}}, \tag{4}$$

We fitted this model (Eq. 4) to our data on fragment occupancy for each primate species and survey period and estimated parameter values (i.e., c, β, and x), using the non-linear regression routines in SPSS. In addition, we calculated all values of A_i and D_i for $J_i = 0.9$ and $J_i = 0.5$ and displayed these incidence lines in the log$A$ on log$D$ scatterplot summary of each species' occupancy. The main trends in primate fragment occupancy were derived from these graphic summaries, mainly because sample size (number of forests) was small and the parameters in the model had large margins of error, diminishing their usefulness.

3. RESULTS

3.1. Forest Use

On average 6.7 households had access to the resources in any given fragment (range 2 to 16). Although there is a correlation between the size of the fragment and the number of households that they support, the strength of the relationship is not strong (r = 0.54, p = 0.040). For example, the largest fragment did support the most households (N = 16), but the second largest fragment only supported two households. Given the fact that the average household in this area contains 4.8 people (NEMA, 1997), these fragments are supporting the fuelwood needs of an average of 32 people. Evidence suggests that the fragments also support a significant share of the neighboring families up to three farms away (>120 families or >576 people, Naughton-Treves, unpub. data).

Estimates of domestic fuel use by people around Kibale indicate that a typical family uses 8.4 kg of fuelwood each day for cooking (Wallmo and Jacobson, 1998). Thus, in one year a local family would use 3,066 kg. (This value is slightly lower than average for non-liquid propane gas users in East Africa; Kammen, 1995.) However, most of the fuelwood gathered for cooking is comprised of fast-growing secondary species like *Acanthus pubescens* and *Vernonia* spp. that are relatively abundant on fallow land (Naughton-Treves and Chapman, 2002).

Commercial uses of the forest involves the extraction of higher volumes of wood and greater long-term impacts given the selection for slow-growing hardwood logs. Extensive clearing of fragments often occurred when neighboring households were engaged in beer brewing (an average of 9.6% of the households were engaged in beer production–8.45 kg per episode, on average 19 times a year), gin (8.8%–875 kg per episode, on average 16 times a year), or charcoal production (14.5%–5935.9 kg per episode, on average 18 times a year). On average 16.2% of the households had cattle or goats.

Just over half of the households (52.8%) that were adjacent to the fragments also had woodlots. We did not have the impression that the fragments where most households did not have woodlots were more degraded than fragments with a number of adjacent woodlots.

3.2. Primate Population Change

Of the 16 fragments that we studied in 1995 that supported resident populations of black-and-white or red colobus, three had been cleared to the extent that primates were no longer present in 2000. The fragments that were cleared had supported five groups of black-and-white colobus (31 individuals total) and were also used by redtail monkeys. For all fragments in 1995 we counted 165 black-and-white colobus, while in 2000 only 118 animals were seen (Figure 1). During the first census, there were 0.405 infants for every adult female, while in the recensus there was only 0.026 infant for every female.

For red colobus the situation was very different. There were seven fragments with red colobus groups in 1995, and none of these fragments were cleared by the time of the 2000 census. In the 2000 census, red colobus groups were found in these original seven fragments and in four additional fragments. In the 2000 census, 159 red colobus were counted and the ratio of infants to adult females was 0.25.

Redtail monkeys were seen or reported by local landowners to be in 18 of the 20 fragments that were surveyed in 1995 and in seven of the 19 surveyed in 2000. They were in fragments that were largely cleared and no longer supported either of the colobine species. Redtail monkeys are known to move between forest fragments and are notorious crop raiders (Naughton-Treves 1997, 1998, Naughton-Treves et al., 1998), thus it seems likely that they used the last few trees of highly degraded fragments to move throughout the landscape while feeding mainly outside of the fragments. Chimpanzees were seen once in 1995 and once in 2000. Evidence of chimpanzees, such as nests, dung, or wadges, was found in nine fragments in 1995 and in five fragments in 2000. Chimpanzees are reported throughout this region and are frequent crop raiders. Blue monkeys and mangabeys were not seen in any of the fragments during either of the surveys. We asked people living near each fragment if they had ever seen or heard blue monkey or mangabeys, both of which have very loud distinct calls, and no one reported them in the area. In fact, while there are Rutoro names for most of Kibale's primates,

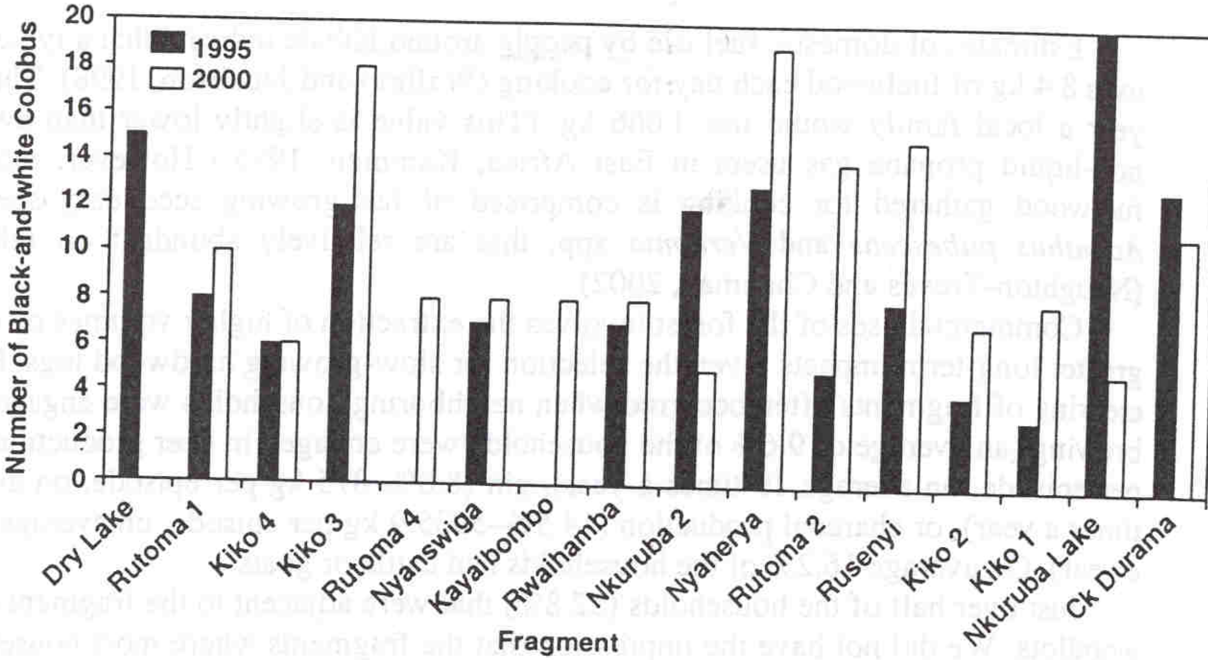

Figure 1. The number of black-and-white colobus found in forest fragments neighboring Kibale National Park, Uganda, in a 1995 and 2000 census.

there is no local name for blue monkeys or mangabeys, suggesting that they have very little contact with them.

3.3. Mainland-Island Incidence-Function Model

Using nonlinear regression we fitted the mainland-island incidence-function model (Eq. 4) to the data. In all cases the ratio of the 'model' sum of squares to the 'error' sum of squares, which is analogous to the F-ratio in linear regression procedures, was greater than four. Thus in all cases the model accounted for a substantial amount of the variance. However, the absolute values of the ratios of the parameter estimates to their standard errors were small (<2), indicating not much confidence in the coefficient values. Thus the curve fits are at best an indication of the trends in occupancy pattern of each primate species and in each survey (Figure 2). Interpretation of the trends is as follows:

Red colobus can persist in fragments that are just over a hectare in size. Occupancy increased with increasing fragment areas, but distance of the fragment from the mainland did not critically affect occupancy. There was little difference in the curves generated from the 1995 and 2000 surveys, with the exception of how the presence of red colobus in distant fragments influenced the curve. Black-and-white colobus are much like the red colobus in being able to persist in very small fragments; however, they are in more fragments than the red colobus. There is very little evidence of a distance effect, yet they are found occupying some of the most distant fragments.

Redtail monkeys exhibited a different pattern. They were found in nearly all the fragments in the 1995 survey and their occupancy was not strongly limited by area or distance. In fact, there were no probability curves for 1995. The curve generated from the 2000 survey suggests that redtail incidence was relatively independent of area and generally decreased with increasing distance from Kibale. This probability curve was in a direction opposite to what would be predicted; that is, incidence is greater for small

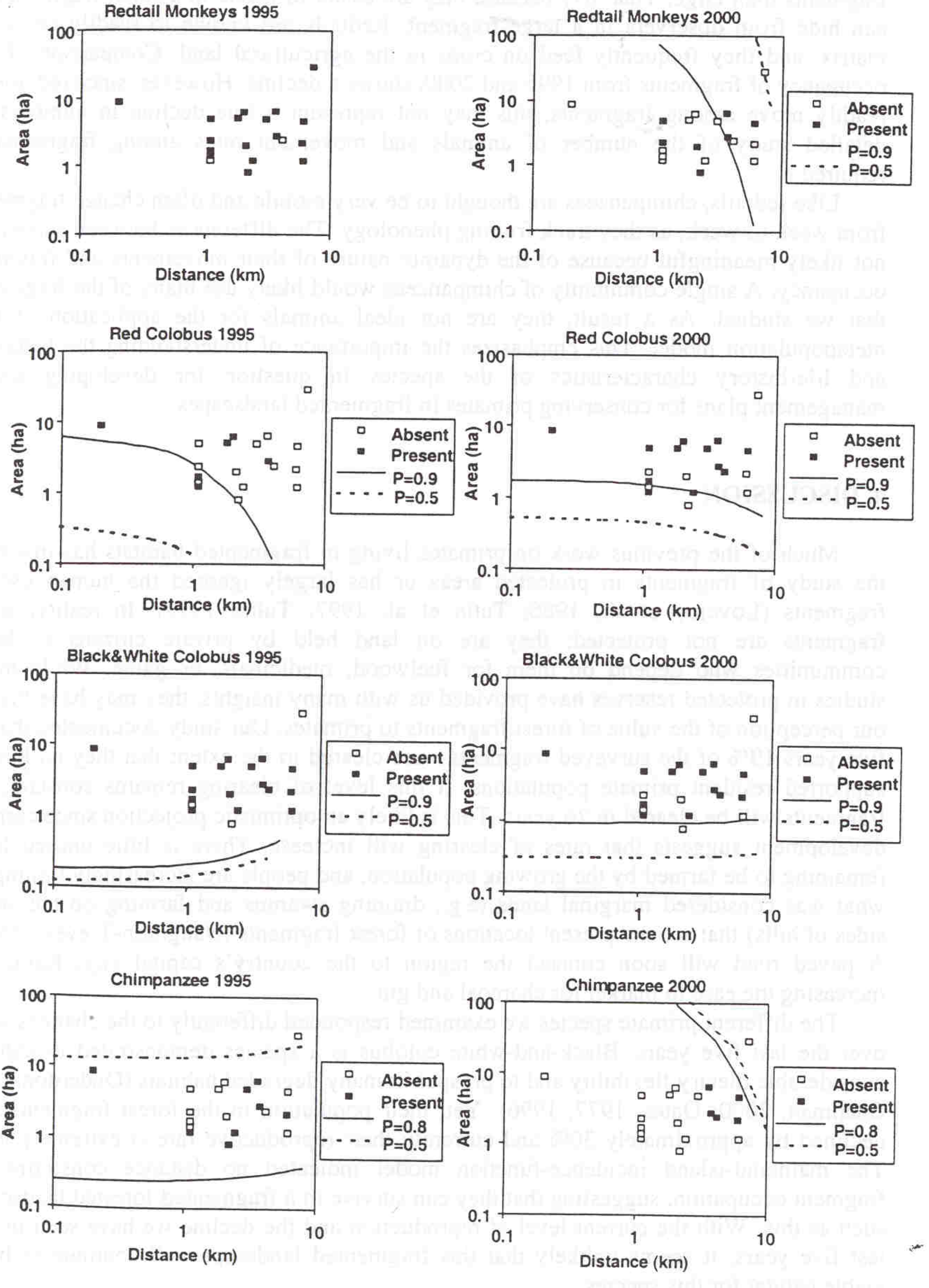

Figure 2. The log-log relationship between area and isolation distance of occupied (solid) and unoccupied (open) forest fragments for four species of primates living in fragments neighboring Kibale National Park, Uganda. The solid and dashed lines provide fitted percent occupancies from logistic equations at different *p* values.

being degraded, it is difficult to envision a reason why their numbers would increase between the two time periods (as indicated by the increased number of fragments they occupy). It is unlikely that they are just now colonizing the fragments that have been there for decades. It is possible that the fragments are operating as a sink and excess animals from the Kibale National Park emigrate to the fragments only to subsequently do poorly in the long term (Pulliam, 1988). However, the ratio of adult females to infants does not support the idea that the fragments are poor-quality sink habitats. With the decline in black-and-white colobus, small groups of red colobus may be more successful in the small fragments. This is supported by 43.2% dietary overlap between a red colobus group range of the red colobus group.

Both redtail monkeys and chimpanzees have similar patterns of use in the fragments and similar mainland-island incidence-functions. We believe that these species are highly mobile, moving readily among fragments, likely tracking the availability of fruit resources. Given this, we are unable to state if the population size of these species or the number of fragments they are occupying have changed over the timeframe of our study. Attempting to apply metapopulation models does not likely provide us any valuable insights into the conservation of these species, but it does highlight the importance of understanding animal behavior and their life-history characteristics for developing sound management plans for conserving primates in fragmented landscapes. These two species are responding to changing conditions at a landscape level and the deforestation of one fragment may have little effect, because animals can travel to alternative fragments. However, if there is general degradation of all fragments and destruction of some, the animals may be negatively affected.

Metapopulation theories are based on the idea that random fluctuations in local populations cause local extinctions and thus unoccupied fragments are available for recolonization (Hanski, 1994; Hanski and Gilpin, 1997). In the forest fragment system we studied, extinctions appear to be driven by increased levels of deforestation that degrade the habitat and make it unsuitable for the primates. Once the fragments are deforested they are used for agriculture and thus are not available for recolonization. Such limitations of metapopulation models have been previously recognized (Thomas, 1994; Lawes et al., 2000). However, despite these limitations, incidence-function metapopulation models provide useful information for the management of animal populations within such fragmented landscapes.

The habitat in this fragmented forest landscape is deteriorating. For black-and-white colobus, evidence indicates that this deterioration is leading to a decline in their population size and poor birth rates. If the situation does not change more fragments will be cleared and the remaining ones will become further degraded. To reverse the present trends would require a major conservation effort, on a scale and of a nature that is not typically done. To stop the fragments from being cleared would require the cooperation of the local people, since this is their land. Alternative sources of income would have to be found (e.g., ecotourism), fuelwood supplies from elsewhere would have to be made available (e.g., a large scale woodlot project), and a great deal of effort would have to be placed in education and outreach to obtain the willing support of all the communities. In all reality, it is unlikely that a project of this magnitude will be initiated. If it is not, it is inevitable that the animals in this fragmented landscape will be lost and the habitat destroyed.

5. SUMMARY

As deforestation and habitat fragmentation accelerate throughout the tropics, the survival of many forest primates depends largely on their ability to cope with such changes. In 1995 we censused 20 forest fragments near Kibale National Park, Uganda, that had existed for several decades. For each fragment we determined the presence or absence of all diurnal primate species and population sizes of black-and-white colobus (*Colobus guereza*). Five years later, we recensused the same fragments and discovered that of the 16 fragments inhabited by primates in 1995, three had been largely cleared and resident primate populations were no longer present. Population declines and lowered fertility rates in the remaining fragments were documented for some species. For example, the black-and-white colobus populations declined from 165 in 1995 to 118 animals in 2000, and there were 0.405 infants per adult black-and-white colobus female in 1995 versus 0.026 infants per female in 2000. For red colobus (*Procolobus badius*) the situation was very different. Red colobus groups occupied seven fragments in 1995, and they were found in an additional four fragments in 2000. In the 2000 census, 159 red colobus were counted and the ratio of infants to adult females was 0.25. The extent of forest clearing in the fragments was documented and factors encouraging clearing are considered. Treating the primates in these forest fragments as putative species metapopulations, we consider whether or not metapopulation principles are useful in conservation planning. In addition, we consider the susceptibility of predictions of species persistence derived from metapopulation principles, and used in management plans, to further human disturbance of forests.

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