

RESEARCH ARTICLE

Evaluating the Suitability of Planted Forests for African Forest Monkeys: A Case Study From Kakamega Forest, Kenya

PETER J. FASHING^{1,2,5*}, NGA NGUYEN^{1,2}, PATRICK LUTESHI³, WINSTONE OPONDO³, JULIE F. CASH¹, AND MARINA CORDS⁴

¹Department of Anthropology, California State University Fullerton, Fullerton, CA

²Environmental Studies Program, California State University Fullerton, Fullerton, CA

³Kakamega Environmental Education Program, Isecheno, Kenya

⁴Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, New York

As natural forest cover declines, planted forests have come to occupy an increasing percentage of the earth's surface, yet we know little about their suitability as alternative habitat for wildlife. Although some primate species use planted forests, few studies have compared primate populations in natural and nearby planted forests. From March 2006 to July 2010, we conducted line transect surveys and assessed group sizes and compositions in natural and nearby 60–70 year old mixed indigenous planted forest to determine the densities of diurnal primate species (*Colobus guereza*, *Cercopithecus mitis*, *C. ascanius*) in these two forest types at Isecheno, Kakamega Forest, Kenya. Line transect data were analyzed using the Encounter Rate, Whitesides, and Distance sampling methods, which all provided broadly consistent results. We found that all three diurnal primate species occupy both natural and planted forest at Isecheno. However, group densities of the two *Cercopithecus* species were 42–46% lower in planted than in natural forest. *Colobus guereza* achieved comparable group densities in the two forest types, although the species is found in smaller groups, and thus at lower (35%) individual density, in planted than in natural forest. Following a logging episode in the planted forest mid-way through our study, *Cercopithecus ascanius* group densities fell by 60% while *C. mitis* and *Colobus guereza* group densities remained stable over the next two years. Overall, our results suggest that while primate species vary in their response to habitat disturbance, planted forest has the potential to contribute to the conservation of some African monkey species. Even for the relatively flexible taxa in our study, however, 60–70 year old mixed indigenous planted forest failed to support densities comparable to those in nearby natural forest. From the perspective of Kakamega's primates, planted forests may supplement natural forest, but are not an adequate replacement for it. *Am. J. Primatol.* 74:77–90, 2012. © 2011 Wiley Periodicals, Inc.

Key words: census; *Cercopithecus*; *Colobus*; density; logging; natural forest; planted forest

INTRODUCTION

Over the past decade, the earth's natural forests have decreased by ~130,000 km² annually, while planted forests (i.e., plantation forests and other types of forests arising primarily from tree planting) have exhibited the opposite trend, increasing by ~50,000 km² each year [Evans, 2009; FAO, 2010]. The destruction of natural forests results primarily from increasing demand for wood products and agricultural land [Lambin et al., 2003]. The expansion of planted forests, in contrast, reflects the growing need to reduce pressure on natural forests as sources of wood, the potential of planted forests for fixing carbon and slowing climate change, and the utility of planted forests in slowing erosion and rehabilitating watersheds [Brockerhoff et al., 2008; Carnus et al., 2006; Lindenmayer, 2009].

The loss of natural forests and concomitant expansion of planted forests have led scientists to begin investigating planted forests as possible suitable habitat for diverse organisms, including many plant, insect, bird, and mammal species. Although nearly half of the earth's planted forest area is found in only four temperate zone nations (China: 24%;

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*Correspondence to: Peter J. Fashing, Department of Anthropology, California State University Fullerton, Fullerton, CA 92834. E-mail: pfashing@fullerton.edu

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Russia: 9%; United States: 9%; Japan: 6%), numerous tropical countries also contain sizable portions of the total planted forest area (e.g., India: 17%; Indonesia: 5%; Brazil: 5%; Thailand: 3%) [Carle et al., 2002; FAO, 2010]. Over the past few decades, many studies have investigated the comparative “biodiversity value” of natural and planted forests for a range of plant and animal species in both temperate [Bonham et al., 2002; Bremer, 2010; Brockerhoff et al., 2008; Fahy & Gormally, 1998; Lantschner et al., 2008; Plough et al., 1987] and tropical regions [Barlow et al., 2007a,b; Bremer, 2010; Brockerhoff et al., 2008; Farwig et al., 2008; Kanowski et al., 2005; Pliosungnoen et al., 2010]. The results of one recent survey of 15 taxonomic groupings in Amazonia suggest that while planted forests provide habitat for many species, the ability to inhabit planted forests varies widely across species and must therefore be studied independently for each taxon, rather than assumed from a few indicator species [Barlow et al., 2007a].

Primates are large, charismatic mammals found in many of the world’s tropical forests, although nearly half of all species are threatened with extinction due to habitat destruction and hunting [IUCN, 2010]. Surprisingly, little research has assessed the suitability of planted forest as habitat for primate taxa, despite recent reports that several species use or even permanently inhabit indigenous or exotic planted forests [Anderson et al., 2007; Merker & Yustian, 2008; Nasi et al., 2008]. Most studies comparing population densities of primate taxa in natural and planted forests have been carried out in SE Asia where natural forests are being felled at alarming rates to make way for palm oil and other plantations [Meijaard et al., 2010; Merker et al., 2005; Pliosungnoen et al., 2010]. The results of these early reports from SE Asia suggest a potentially promising role for planted forests in primate conservation in this region, although continued monitoring of these populations is needed to assess the long-term viability of primate communities (i.e., their ability to survive and reproduce through time) that partially or exclusively inhabit planted forests.

Studies of a wider array of species in additional forested regions of the world are needed to assess the “biodiversity value” of planted forests for primates. Like other tropical regions, Africa has suffered severe deforestation in recent decades and only a fraction of its original forest cover remains [FAO, 2010]. Planted forests cover > 150,000 km² in Africa, with 61% of this area consisting primarily of indigenous tree species [FAO, 2010], yet the utility of these forests for primate conservation is essentially unknown. Planted forests of mixed indigenous species, particularly those established during the colonial era which have had a long time to grow [Oates, 1999; Okali & Eyog-Matig, 2004], might be

expected to provide especially promising habitat for primates and other forms of wildlife.

In this study, we aimed to evaluate the potential of old (60–70 years) planted forest to provide suitable habitat for three species comprising a diurnal primate community in East Africa. In particular, we sought to determine which, if any, of the species reached comparable densities in planted and natural forest. Using data collected over a 52-month period via line transect censuses and assessments of group size and composition, we compared measures of abundance for primate species in natural (old secondary forest) and nearby mixed indigenous planted forest around Isecheno study site in the Kakamega Forest, Kenya. The three primate species in this study, eastern black and white colobus monkeys (*Colobus guereza*), blue monkeys (*Cerco-pithecus mitis*), and redtail monkeys (*C. ascanius*) have relatively wide distributions in the tropical forests of Africa and are typically regarded as “generalists” who sometimes fare well in disturbed habitats [Chapman et al., 2005; Johns & Skorupa, 1987; Plumptre & Reynolds, 1994]. As a result, we predicted that all three species would occur in planted forest and that their densities in planted forest would approach those in nearby natural forest. In addition, mid-way through our study, a logging event unfortunately took place in a section of the planted forest, enabling us to assess the early responses to logging of each species in this habitat. While the results reported here are based on a case study conducted over a limited geographical area, our study at Kakamega Forest provides the first quantitative comparison of African primate populations in natural versus planted forest and makes a case for the increasing importance of studying primates in planted forest habitats.

METHODS

Study Site

The Kakamega Forest (0°19'N 34°52'E; Elev. 1,580 m) covers 238 km², of which 133 km² is forested, consisting of old secondary forest, young secondary forest, mixed indigenous plantation forest, and monoculture indigenous or exotic plantation forest [Mitchell et al., 2009]. As the only remaining area of Guineo-Congolian rainforest in Kenya, Kakamega Forest is of major conservation importance and home to many species of plants, birds, reptiles, and insects found nowhere else in the country [Mitchell et al., 2009]. Kakamega is also one of Kenya’s most species-rich forests for primates, with five diurnal species (*Colobus guereza*, *Cerco-pithecus ascanius*, *C. mitis*, *C. neglectus*, and *Papio anubis*) and one nocturnal species (*Perodicticus potto*). However, because *Perodicticus potto* is nocturnal, *C. neglectus* does not inhabit our study area, and *Papio anubis* is an infrequent visitor to our

study area (they were observed only once during censuses—in natural forest), we included only *Colobus guereza*, *Cercopithecus mitis*, and *C. ascanius* in our study. Between 1990 and 2006, mean annual rainfall for the forest was 1915 mm and mean annual temperature was 18.7°C [Mitchell et al., 2009].

Primate censuses occurred in both “natural forest” and “planted forest” (Fig. 1). Our “natural forest” study area (Fig. 1) consisted of ~2 km² of old secondary forest located north of the Isecheno Forest Station that was contiguous with most of the remaining natural forest (~120 km²) at Kakamega [Cords, 1987; Fashing et al., 2004; Mitchell et al., 2009]. Selective logging for economically valuable timber species [e.g., *Croton megalocarpus* (Euphorbiaceae), *Olea capensis* (Oleaceae), *Aningeria altissima* (Sapotaceae)] occurred in the natural forest in the 1930s and 1940s and low levels of enrichment planting (several stems per ha) of indigenous [e.g. *Olea capensis* (Oleaceae), *Khaya anthotheca* (Meliaceae)] and exotic species [e.g. *Bischofia javanica* (Euphorbiaceae), *Acrocarpus fraxinifolius* (Leguminosae)] were carried out in gaps created by logging [Mitchell, 2004; Mitchell et al., 2009]. Major disturbance of this area has not occurred since the 1940s, although illegal exploitation by local people continues at low-to-moderate levels in the form of tree felling for poles, liana cutting for removal of dead firewood, charcoal

burning, and honey harvesting [Bleher et al., 2006; Fashing et al., 2004; Mitchell, 2004]. A comparison of tree stem densities in the study area between 1981 and 1999 revealed a 21% decrease in pioneer species and increases in the stem densities of many climax species, suggesting that the forest is still recovering from the selective logging of the 1930s and 1940s [Fashing et al., 2004].

Our “planted forest” study area (Fig. 1) was located south of the “natural forest” study area to which it was connected by a corridor of younger regenerating natural forest. The planted forest consists of ~2 km² of mostly mixed indigenous trees [primarily *Prunus africana* (Rosaceae), *Olea capensis* (Oleaceae), *Maesopsis eminii* (Rhamnaceae), *Zanthoxylum gillettii* (Rutaceae), *Cordia africana* (Boraginaceae), and *Markhamia lutea* (Bignoniaceae)] planted in the 1930s and 1940s in open glades or where natural forest in the area had been clear cut [Mitchell, 2004, pers. comm.]. The forest in this area was left to regenerate, while enduring the same forms of disturbance characteristic of the nearby natural forest over the past 60–70 years. It is likely that birds and other animals from nearby natural forest have dispersed seeds of additional indigenous species not planted by foresters [Farwig et al., 2009], many of which can be seen as trees in the subcanopy and other lower strata in the planted forest today [e.g., *Albizia gummifera* (Mimosaceae)]. Most of the planted forest can thus be regarded as relatively old and without additional major disturbance may transition over time to forest akin to natural forest [Evans & Turnbull, 2004], a pattern well described for European forests [Brockerhoff et al., 2008].

Unfortunately, over a one-week period in mid-June 2008, a portion of the planted forest near the southern edge of the east-west census route (that passed through the heart of the planted forest) was logged for the installation of power lines. This 15–20 m wide swathe stretched along nearly 1,800 m of the planted forest census route, eliminating ~0.03 km² of planted forest. Our census dataset for the planted forest has thus been divided into two roughly equal time periods for analysis: ~2 years before and ~2 years after logging.

Data Collection

The research in our study was purely observational and adhered to both the legal requirements of Kenya and the American Society of Primatologists Principles for the Ethical Treatment of Non Human Primates.

Line transect surveys

Between March 2006 and July 2010, we conducted 113 line transect surveys along a 2.883 km census route through natural forest. Over the same period, we carried out 117 line transect surveys (62

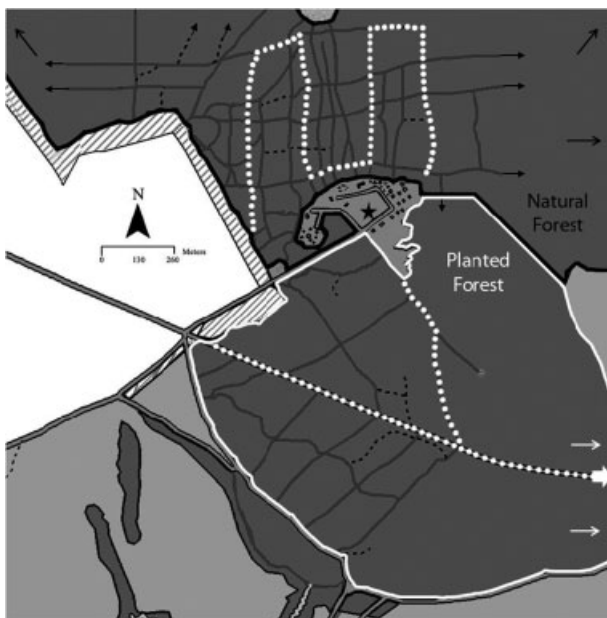


Fig. 1. Map depicting location of transect routes (indicated by white dots) in the natural (outlined in black) and planted forest (outlined in white) areas around Isecheno study site, Kakamega Forest, Kenya. The thin black and white arrows indicate that the forest areas continue beyond where the map ends; the thick white arrow indicates that the planted forest transect continues beyond where the map ends; gray lines in both forest types indicate the locations of pre-existing trails; // = tea plantation; ★ = Isecheno village.

before logging and 55 after logging) along a 2.415 km census route through planted forest. To limit the impact of seasonal factors on abundance estimates [Struhsaker, 1981], we sampled evenly across the seasons conducting an average of 2.2 censuses per month in natural forest and 2.3 censuses per month in planted forest. Although a larger number of transects in each forest type would have improved the study design [Buckland et al., 2010a], practical considerations, including the local forester's policy against cutting new trails, limited us to a single census route in each forest type. Our transects followed pre-existing linear footpaths or dirt roads 1–5 m in width, though at times the routes followed nonlinear (e.g. inverse U-shaped) trajectories. The trails used as transects passed through representative stretches of each forest type and were characterized by flat topography similar to surrounding forest areas. Monkeys in both forest types ranged from partly to fully habituated to the presence of observers, and showed no overt signs of avoiding humans along the transects.

Census walks began between 09:00 and 11:00. Once a monkey was spotted, it was observed from the transect path for up to 10 min to determine whether it belonged to a mixed-sex group, or whether it was a solitary male or a member of an all-male band. The following data were recorded for monkeys observed along the transect: (1) time of sighting, (2) initial cue of detection (auditory or visual; those infrequent occasions when monkeys were heard but not eventually seen were not recorded), (3) location along census route, (4) species sighted, (5) number of monkeys sighted, (6) perpendicular transect to animal distance, and (7) observer to animal distance. For sightings of groups, only the distance to the first individual spotted was recorded since the high density of monkeys at Isecheno made it impractical to record the distance to every individual as recommended by some census techniques [Buckland et al., 2010a]. Given the extent to which differences in ability to spot monkeys and estimate distances to them can influence density estimates [Mitani et al., 2000], we devoted considerable effort to achieving high inter-observer reliability. PJF trained each of the individuals (PL, WO) walking census transects and all observers routinely practiced estimating distances to monkeys and other objects together.

Group size and composition

Because line-transect census methods dictate that ≤ 10 min should be spent with each group sighted along the transect route, the number of individuals counted in monkey groups during censuses often represent substantial underestimates [Struhsaker, 1981], especially in groups of moderate or large size, or those that are not cohesive. As a result, we conducted additional observations outside

of censuses to obtain reliable group size and composition data for multiple groups of *Colobus guereza* in natural (June 2008; $n = 7$ groups) and planted forest (December 2009; $n = 6$ groups). The composition of each *C. guereza* group was determined on 3–5 occasions until the same composition was obtained repeatedly. Members of each group were assigned to the categories of adult male, adult female, juvenile, and infant. Using the same classification scheme, group sizes and compositions were obtained for three groups of *Cercopithecus mitis* in natural forest from MC's long-term monitoring records for this population [Cords & Chowdhury, 2010]. To be consistent with the method used for *C. guereza*, we selected a random month in the middle of the census period, July 2008, as representative of group size and composition for *C. mitis* in natural forest. Quantitative data on group size and composition were not available for multiple groups of *C. mitis* in planted forest, although groups in this forest appeared to be no larger and probably smaller than those in natural forest [Cords, pers. observ.]. Data on group size and composition were not available for *C. ascanius* in either natural or planted forest during the study period. Since groups of *Colobus guereza* and *Cercopithecus mitis* remain fairly stable in size over time, with the only major fluctuations occurring during relatively infrequent group fission events [Cords, in press; Cords & Rowell, 1986], we consider group size estimates mid-way through the study to be representative for these species during the study period.

Data Analysis

Encounter rate and group density

We analyzed the line transect data collected in this study using three common techniques to obtain estimates of group abundance for each monkey species in the different forest types at Isecheno. Our rationale for analyzing census data in multiple manners is that this approach enables comparisons of our results from Isecheno with a broader array of studies of primates and other wildlife than if only a single method had been used. Since they are not incorporated into calculations of abundance for group-living animals in most analysis techniques, sightings of bachelor (i.e., nonresident) males were excluded from all analyses of group abundance (although we did carry out a separate analysis of the relative abundance of bachelor males in different forest types, see below).

The first measure of abundance that we calculated was encounter rate, or the mean number of groups observed per km walked, a conservative technique for estimating abundance favored by several primate researchers [Mitani et al., 2000; Rovero et al., 2006]. Second, we calculated group density using the Whitesides method, a technique

that incorporates species-specific mean group spread into transect width estimation [Whitesides et al., 1988]. This technique has been demonstrated previously to produce consistently accurate group density estimates for multiple primate species at Isecheno [Fashing & Cords, 2000]. The rationale and formula for using the Whitesides method are described in detail in Whitesides et al. [1988] and Fashing and Cords [2000]. Third, we calculated group density using a version of the popular Distance method recommended for use in primates and other forest-dwelling, group-living animals [described in detail in Buckland et al., 2010a; Thomas et al., 2010].

To ensure consistency with many previous primate census studies and confirm that we had carried out enough transect walks to reach an asymptote in group encounter rate, we estimated the precision of group encounters after each transect walk [Mammides et al., 2009; Struhsaker, 1981; Teelen, 2007]. This measure consists of “the 95% confidence limits of estimated means expressed as the percentage of these means” [Struhsaker, 1981: 52]. In practice, as the sample size of census walks increases, percentage precision tends to become lower (i.e., the estimated group encounter rate becomes more precise) [Struhsaker, 1981]. Our estimations of group density using both the Whitesides and Distance methods incorporated a measure of mean group spread for each monkey species. In the absence of new data, we used identical group spread values (*Colobus guereza*: 22 m; *Cercopithecus ascanius*: 56 m; *C. mitis*: 109 m) to those in a previous study we carried out at Isecheno [Fashing & Cords, 2000]. While mean group spread may vary over time for some primate populations [Plumptre, 2000], evidence from studies conducted many years apart at Kakamega suggests that mean group spread has remained relatively stable within species at this site [Cords, 1987; Fashing & Cords, 2000; Miller, 2010]. In using the Distance method, we followed the advice of Buckland et al. [2010a: 840] in incorporating the measure of mean group spread by setting the corrected perpendicular sighting distance “equal to the recorded perpendicular distance multiplied by $1 + (\bar{r}/\text{AOD})$ where \bar{r} is half the mean group spread and AOD is the animal to observer distance”.

Analyses using the Distance method were carried out with Distance 6.0 Release 2 [Thomas et al., 2010]. For each species in each forest type, we carried out analyses with several detection probability functions before choosing the density estimate produced by the function with the lowest Akaike’s Information Criterion (AIC) value [Buckland et al., 2001]. In all instances, the hazard rate function with cosine adjustment provided the lowest AIC values, although in most cases, other functions generated similar density estimates. In several instances, truncation of sightings at an animal-transect distance where sightings became

much less common reduced outliers and facilitated better modeling of the data (i.e., produced lower AIC values) [Buckland et al., 2001].

Because censuses were carried out in each forest type only twice per month on average, the number of monkey sightings was generally too small to enable meaningful evaluation of seasonal or yearly variation.

Individual density and biomass

We calculated individual densities by multiplying group density by mean group size for the species for which group size data were available (i.e., *Colobus guereza* in natural and planted forest; *Cercopithecus mitis* in natural forest). We also calculated biomass for these species by multiplying group density by the mass of an average sized group [Fashing & Cords, 2000; Oates et al., 1990]. Adult body weight values were taken from Harvey et al. [1987]. Subadult male body weight was estimated to equal that of adult females, and juvenile body weight was estimated to equal one-half of adult female weight [Fashing & Cords, 2000; Oates et al., 1990]. We estimated infant body weight by adding the neonate weight provided in Harvey et al. [1987] to juvenile body weight and dividing by two [Fashing & Cords, 2000].

Bachelor male encounter rate

While bachelor males (i.e., individuals that are typically solitary and do not live in mixed-sex groups) are excluded from most analyses of line transect census data on group-living animals [Whitesides et al., 1988], crude measures of abundance for these individuals can sometimes be informative in other ways [Felton et al., 2003]. Therefore, to obtain a rough indication of whether bachelor male abundance differs between forest types, we calculated encounter rates (individuals per km of transect walked) for bachelor males of each monkey species around Isecheno.

RESULTS

Estimates of Precision Over Time

For all three monkey species (*Cercopithecus mitis*, *C. ascanius*, and *Colobus guereza*) in all three forest types (natural forest, planted forest before logging, and planted forest after logging), estimates of precision leveled off well before the last census walk, suggesting that additional censuses would have had minimal impact on our estimates (Fig. 2). Reflecting the relative encounter rates with groups of each species (see below), precision estimates were consistently lowest (best) for *Colobus guereza*, intermediate for *Cercopithecus mitis*, and highest for *C. ascanius*.

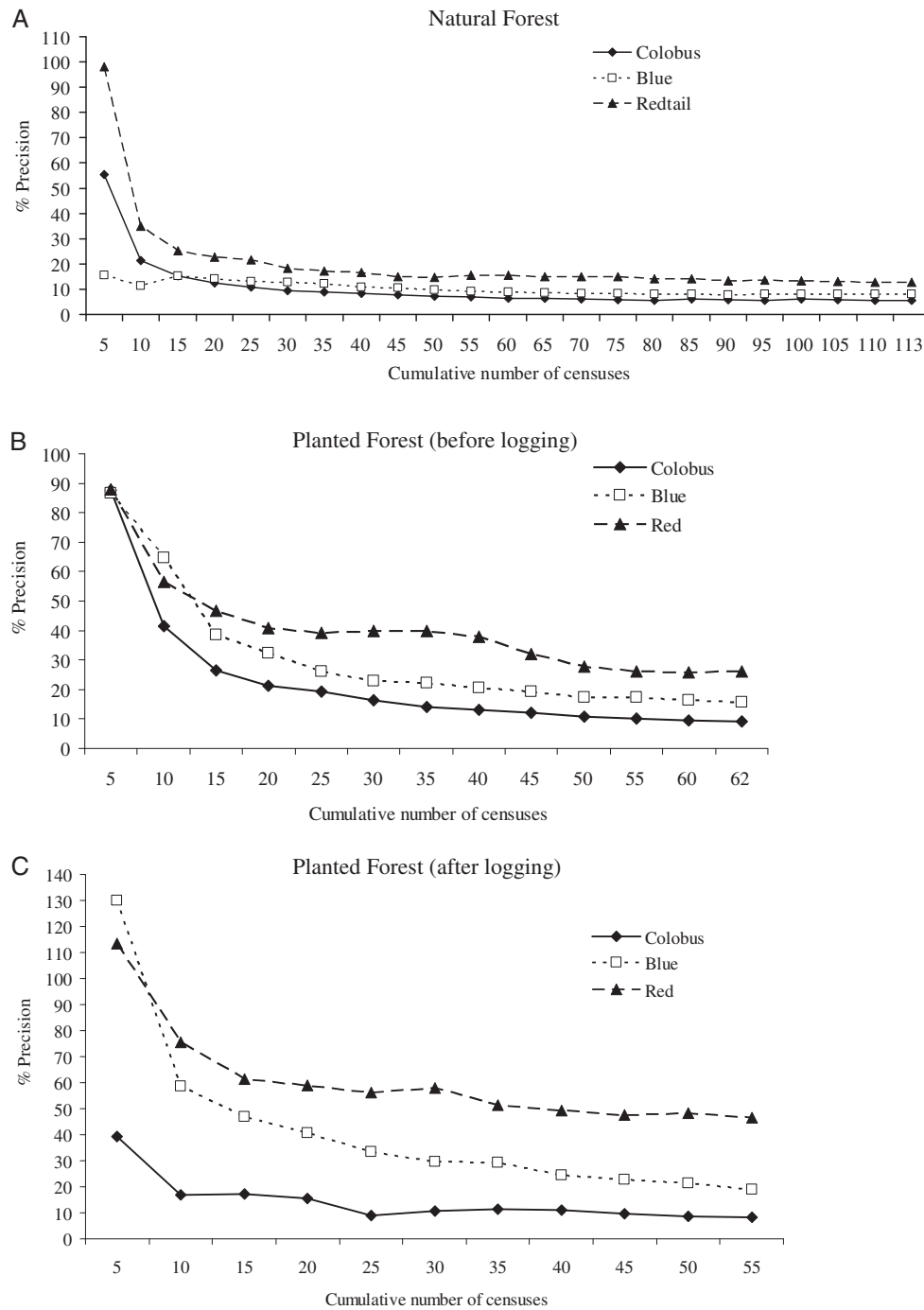


Fig. 2. Precision analyses for the mean number of groups per census in each of the three different forest types as a function of the cumulative number of censuses completed. % precision = (95% confidence limits/mean number of groups per census) \times 100, as described in Struhsaker [1981].

Estimates of Group Abundance Generated by Different Techniques

Group density estimates generated by the Whitesides and Distance methods were remarkably consistent with one another for *Cercopithecus mitis* and *C. ascanius* (Table I). Estimates for *Colobus*

guereza were also broadly similar across the group density estimation techniques, exhibiting no more than a 13% difference between techniques in any of the forest types. Although not directly comparable numerically given the different units of measurement, the general pattern for encounter rate was also largely consistent with the patterns for group

TABLE I. Abundance Estimates Calculated (a) as Encounter Rate (grps/km Walked), (b) via the Whitesides Method (grps/km²), and (c) via the Distance Method (grps/km²) for the Three Diurnal Monkey Species at Isecheno in Natural Forest ($n = 113$ Censuses), Planted Forest Before Logging ($n = 62$ Censuses), and Planted Forest After Logging ($n = 55$ Censuses).

Species	Forest type	Encounter rate			Whitesides method			Distance method		
		Grps/km	95% C.L.	Density (grps/km ²)	SE	Density (grps/km ²)	SE	95% C.L.	C.V. (%)	
<i>Colobus guereza</i>	Natural	1.69	1.60-1.79	11.7	0.3	13.2	0.5	12.4-14.2	3.4	
	Planted (pre-logging)	1.45	1.32-1.59	11.2	0.3	12.1	0.8	10.7-13.7	6.3	
<i>Cercopithecus mitis</i>	Planted (post-logging)	1.28	1.18-1.39	11.2	0.3	10.7	0.7	9.4-12.2	6.4	
	Natural	0.95	0.88-1.03	5.0	0.1	4.6	0.2	4.2-5.0	4.7	
<i>Cercopithecus ascanius</i>	Planted (pre-logging)	0.57	0.48-0.66	2.9	0.0	3.0	0.3	2.5-3.6	9.2	
	Planted (post-logging)	0.59	0.49-0.71	2.9	0.1	2.9	0.3	2.3-3.5	10.4	
	Natural	0.58	0.51-0.66	3.7	0.1	3.6	0.3	3.0-4.1	7.7	
	Planted (pre-logging)	0.28	0.22-0.36	2.0	0.1	2.1	0.3	1.5-2.9	16.0	
	Planted (post-logging)	0.10	0.06-0.16	0.8	0.1	0.8	0.2	0.5-1.3	24.5	

density using the Whitesides and Distance methods. Because we have validated the Whitesides method for monkeys at Kakamega in the past [Fashing & Cords, 2000], we used the results generated by this method to make density comparisons between species and forest types.

Group Density Across Monkey Species and Forest Types

All three monkey species were present in each of the forest types. *Colobus guereza* had by far the highest group densities and *Cercopithecus ascanius* had the lowest group densities in each forest type (Table I).

Group densities of the two *Cercopithecus* species were markedly lower in planted than in natural forest. *Cercopithecus mitis* group density in planted forest before logging was 42% lower than in natural forest (2.9 grps/km² vs. 5.0 grps/km²) and group density for this species in planted forest did not change after logging (Fig. 3). Similarly, *Cercopithecus ascanius* group density was 46% lower in planted forest before logging than in natural forest (2.0 grps/km² vs. 3.7 grps/km²). However, *C. ascanius* group density in planted forest declined by 60% after logging (0.8 grps/km² vs. 2.0 grps/km²) (Fig. 3).

In contrast, *Colobus guereza* group density remained relatively stable across the three forest types. Group density for this species in planted forest before logging was 4% lower than in natural forest (11.2 grps/km² vs. 11.7 grps/km²), and remained unchanged following logging in the planted forest (Fig. 3).

Group Sizes, Individual Densities, and Biomass Across Forest Types

On average, *Colobus guereza* group sizes in logged planted forest (mean = 9.7; range = 7-13;

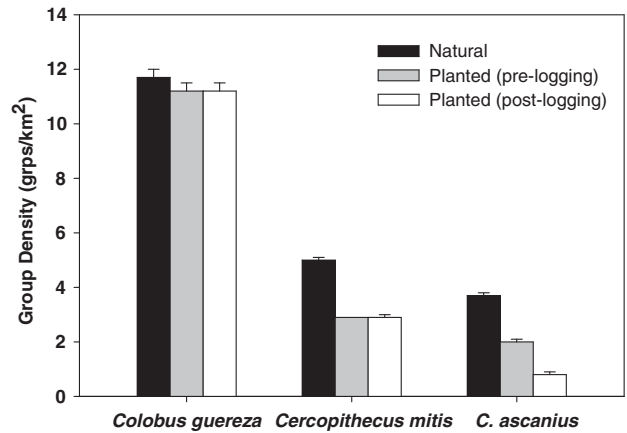


Fig. 3. A comparison of group densities (\pm standard error) calculated via the Whitesides method for the three diurnal primate species in natural forest, planted forest before logging, and planted forest after logging.

$n = 6$ groups) were 33% smaller than in natural forest (mean = 14.4; range = 8–22; $n = 7$ groups) (Table II). No data are available on *C. guereza* group sizes in planted forest before logging. Individual density for *C. guereza* in logged planted forest was 35% lower than in natural forest (109 ind/km² vs. 168 ind/km²). Consequently, biomass for *C. guereza* in logged planted forest was 40% lower than in natural forest (830 kg/km² vs. 1388 kg/km²).

Cercopithecus mitis groups averaged 38.3 individuals (range = 20–52; $n = 3$ groups) in natural forest (Table II). Although no quantitative data are available on group sizes in planted forest during any period, blue monkey groups in planted forest appeared to be no larger, and were probably smaller, than in natural forest (M. Cords, pers. observ.). Individual density and biomass were 192 ind/km² and 583 kg/km², respectively, for *C. mitis* in natural forest.

Bachelor Male Encounter Rates Across Species and Forest Types

Encounter rates with bachelor males (Fig. 4) were many times lower than encounter rates with mixed-sex groups (Table I) for all species in all forest types. Sightings of bachelor males of *Colobus guereza* were particularly scarce in all forest types (Fig. 4). We encountered bachelor male *Cercopithecus mitis* and *C. ascanius* far more often in natural forest than in planted forest; these males were especially rare in planted forest after the logging event (Fig. 4).

DISCUSSION

We found that 60- to 70-year-old mixed indigenous planted forest near the Isecheno study site in the Kakamega Forest, Kenya provides habitat for resident groups of the three diurnal primate species (*Colobus guereza*, *Cercopithecus mitis*, *C. ascanius*) that also permanently inhabit nearby natural forest. However, of the three primate species occurring around Isecheno, only *Colobus guereza* achieved similar group densities in planted and natural forest. In contrast, group densities of the two *Cercopithecus* species were 42–46% lower in planted forest. Even *Colobus guereza* exhibited 33% smaller mean group sizes in planted forest, which resulted in a substantially lower (35%) individual density in planted than in natural forest. A logging episode in the planted forest at Isecheno mid-way through our study enabled us to evaluate the short-term responses of the three primate species to selective logging. Over the next two years, *Colobus guereza* and *Cercopithecus mitis* group densities remained stable, while *C. ascanius* group densities fell by 60%, suggesting a greater sensitivity to logging in the latter species.

We also found strong concordance between group density estimates produced from line transect census data analyzed with both the Whitesides

TABLE II. Group Density, Mean Group Size, Mean Group Mass, Individual Density, and Biomass for *Colobus guereza* and *Cercopithecus mitis* (Group Size Was Unknown for *C. mitis* in Planted Forest and for *C. ascanius* in Both Forest Types.)

	Group density ^a (grps/km ²)		Mean group size (# ind)		Mean group mass (kg)		Individual density (ind/km ²)		Overall biomass (kg/km ²)	
	Natural	Planted	Natural	Planted	Natural	Planted	Natural	Planted	Natural	Planted
<i>Colobus guereza</i>	11.7	11.2	14.4	9.7	118.6	74.1	168	109	1388	830
<i>Cercopithecus mitis</i>	5.0	2.9	38.3	–	114.3	–	192	–	583	–

^aCalculated using the Whitesides method.

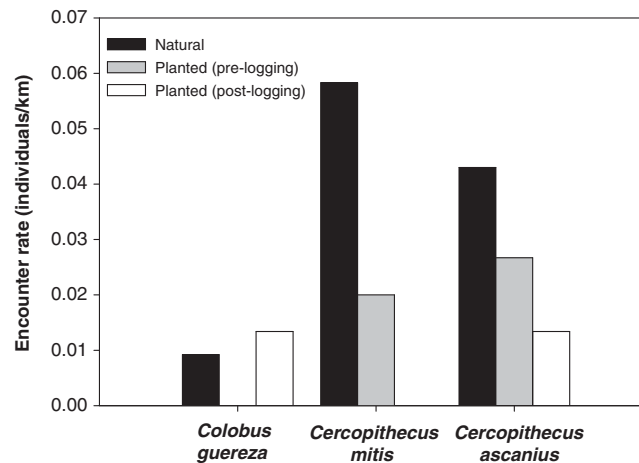


Fig. 4. A comparison of encounter rates (individuals sighted per kilometer walked) for bachelor males of the three diurnal primate species in natural forest, planted forest before logging, and planted forest after logging.

method and a recently proposed modification of the Distance method that incorporates mean group spread into density estimates. Our results suggest that these techniques produce generally comparable group density estimates though additional comparisons of these techniques in other forests of known primate densities would be valuable.

Planted Forests as Primate Habitats

All three diurnal monkey species at Kakamega Forest occur at substantially higher densities in natural forest than in planted forest. Of the four studies prior to ours that compared densities of primates in natural and nearby planted forests, two reported higher primate densities in natural forest (Table III). For example, densities of *Macaca fuscata* at Yakushima, Japan were twice as high in both primary and logged natural forest than in an indigenous monoculture planted forest [Hanya et al., 2005]. In addition, *Tarsius diana*e at Lore-Lindu, Sulawesi was four times more abundant in minimally disturbed natural forest than in mixed exotic planted forest and cropland [Merker et al., 2005]. Furthermore, although he did not calculate population densities, Ganzhorn [1987] provided evidence that seven lemur species (*Avahi laniger*, *Cheirogaleus major*, *Hapalemur griseus*, *Indri indri*, *Lemur fulvus*, *Lepilemur mustelinus*, and *Microcebus rufus*) surveyed at Analamazoatra, Madagascar were all much more abundant in natural forest than in old exotic *Eucalyptus* plantations with understories consisting of regenerating indigenous forest. In addition Ganzhorn [1987] found that no lemurs occurred in young (<25 year old) *Eucalyptus* forest lacking indigenous understory.

It is important to note, however, that planted forest may not necessarily be inferior habitat to natural forest for all primates or at all locations (Table III). For example, Pliosungnoen et al. [2010]

recently found that densities of *Nycticebus bengalensis* at Khao Ang Rue Nai, Thailand were slightly higher in 15- to 18-year-old planted forest containing two exotic species and a naturally regenerating indigenous understory than in relatively undisturbed natural forest [Pliosungnoen et al., 2010]. While Pliosungnoen et al. [2010] do not mention whether *N. bengalensis* actually consumed the exotic planted species, they do note that several regenerating indigenous tree and liana species reached high levels of abundance in the planted forest and provided major sources of food for this primate.

Pongo pygmaeus in East Kalimantan were also recently reported to occur at similar densities in young, exotic, and species-poor pulp and paper plantations as in nearby “natural forests” [Meijaard et al., 2010]. This result, which the authors were careful to note as “preliminary” [Meijaard et al., 2010], is particularly surprising given the orangutan’s diverse and highly frugivorous diet [Russon et al., 2009] and its sensitivity to anthropogenic disturbance [Felton et al., 2003; Morrogh-Bernard et al., 2003], factors that have contributed to its designation as an endangered species [Ancrenaz et al., 2008]. Given that the forests described as “natural forest” in Meijaard et al.’s surveys were, in fact, “highly degraded” [Meijaard et al., 2010], additional comparisons of *P. pygmaeus* in planted forest with those in undisturbed or less disturbed natural forest are urgently needed to more thoroughly evaluate the suitability of planted forests for this species.

Intriguingly, the two studies to date that have provided evidence of primates existing at comparable densities in planted and natural forest were conducted on solitary species occurring at relatively low individual densities (i.e., <5 individuals/km²) [Meijaard et al., 2010; Pliosungnoen et al., 2010], a pattern that suggests that planted forest located near natural forest may provide suitable habitat for

TABLE III. Comparison of Primate Population Densities in Natural and Planted Forests Across the Five Sites for Which Published Data Are Available.

Study site	Study duration (months)	Species	Condition	Natural forest			Planted forest		
				Grp density (grps/km ²)	Indiv Density (ind/km ²)	Genera planted	Condition	Grp density (grps/km ²)	Indiv density (ind/km ²)
SRH & SHJ, East Kalimantan ^a	7	<i>Pongo pygmaeus</i>	Heavy disturbance	-	1.34-1.76	<i>Acacia</i> , <i>Eucalyptus</i>	1- to 5-yr-old two exotic spp.	-	1.45
Khao Ang Rue Nai, Thailand	14	<i>Nycticebus bengalensis</i>	Some disturbance	-	4.00	<i>Acacia</i> , <i>Leucaena</i>	15- to 18-yr-old two exotic spp. 7- to 14-yr-old two exotic spp.	-	4.26
Lore-Lindu, Sulawesi	17	<i>Tarsius dianae</i>	Minimal disturbance	57	268	<i>Gliricidia</i> , <i>Theobroma</i> , <i>Bambusa</i> , <i>Imperata</i> , <i>Zea</i>	Mixed exotic spp. and crops	14	45
Yakushima, Japan	37	<i>Macaca fuscata</i>	Undisturbed	1.1	27	<i>Cryptomeria</i>	19- to 27-yr-old single indigenous sp.	0.7	14
Kakamega Forest, Kenya	52	<i>Colobus guereza</i> <i>Cercopithecus mitis</i> <i>Cercopithecus ascanius</i>	Logged Some disturbance Some disturbance	2.1 11.7 5.0	27 168 192	<i>Prunus</i> , <i>Olea</i> , <i>Maesopsis</i> , <i>Zanthoxylum</i> , <i>Cordia</i> , <i>Markhamia</i>	Pre-logging 60- to 70-yr-old mixed indigenous spp. (before logging) Post-logging Pre-logging Post-logging Pre-logging Post-logging	11.2 11.2 2.9 2.9 2.0 0.8	- 109 - - - -

^aStudy was conducted at Surya Hutani Jaya (SRH) and Sumalindo Hutani Jaya (SHJ) in East Kalimantan, Indonesia.

solitary primates typically found at very low individual densities. Because study duration may influence density estimates [Struhsaker, 1981], however, it is worth noting that these two studies were shorter in duration than the three that found primates living at much higher densities in natural than in planted forest (Table III).

While it is encouraging that the list of primate species capable of using planted forests is growing [Table III; Dela, 2007; Ganzhorn, 1987; Ganzhorn & Abraham, 1991; Nasi et al., 2008], more intensive work is needed to assess whether primate populations in these forests are capable of surviving over the long-term. Intensive behavioral ecological studies of planted forest primates have rarely been conducted [e.g., Dela, 2007], making it difficult to assess the extent to which groups or individuals found in planted forest (a) are full-time residents or temporary migrants to these areas, and (b) actually rely on the planted tree species for food and other resources essential to survival and reproduction. To facilitate comparisons across studies, it is also critical that primatologists provide as much detail as possible about the age and species composition of planted (and natural) forest habitats, their past and present disturbance regimes, and their distance from natural forest.

Given that the percentage of the world's forested areas accounted for by planted forests is projected to continue to increase over time [FAO, 2010], and that primates vary in their ability to inhabit and thrive in planted forests (Table III), more funding for studies of primates in these nontraditional habitats would be valuable. Indeed, there is little doubt that the long-term conservation prospects for many primate species will hinge partly on their ability to utilize planted forests not only as corridors between fragments of natural forest but, in some cases, as their primary habitats.

At the same time, we wish to emphasize our finding that even in a forest consisting of multiple indigenous tree species planted 60–70 years ago and allowed to regenerate without major disturbance, three “generalist” arboreal monkey species failed to reach densities approaching those observed in nearby natural forest. Thus, as long as it is still possible, the retention of natural forest (primary, secondary, or both) must be considered the top immediate priority for the conservation of forest-dwelling primates.

Short-Term Impacts of Logging on Primates

Numerous studies have demonstrated that logging has adverse long-term impacts on most primate species. These impacts may include reductions in population density [Johns & Skorupa, 1987; Waltert et al., 2002], group size [Struhsaker, 1997], or body mass [Olupot, 2000] as well as increases in parasite prevalence, species richness, or infection risk [Gillespie et al., 2005]. Not all primates are equally affected by logging, however, and a few taxa actually

exhibit increases in population density following the selective logging of their habitat [Johns & Skorupa, 1987; Plumptre & Reynolds, 1994; Skorupa, 1986]. Indeed, the species examined in our study at Kakamega, *Colobus guereza*, *Cercopithecus mitis*, and *C. ascanius*, are known from previous studies in Uganda to sometimes fare better in logged than in unlogged forest [Chapman et al., 2005; Plumptre & Reynolds, 1994; Skorupa, 1986], suggesting they may be more flexible ecologically than many other forest primates. In Plumptre and Reynolds's [1994] study at Budongo, for example, all three species occurred at higher densities in logged forest than in unlogged forest. At Kibale, in contrast, results for these species were more varied. *Colobus guereza* consistently occurred at higher densities in logged plots than in unlogged plots, *Cercopithecus ascanius* occurred at higher densities in some logged plots and lower densities in others, and *C. mitis* consistently occurred at lower densities in logged plots [Chapman et al., 2005; Skorupa, 1986].

The logging event that occurred near our transect in planted forest half-way through our study offered us the opportunity to examine the short-term impacts of logging on these species at Kakamega. During the two years following logging, group densities remained stable for *Colobus guereza* and *Cercopithecus mitis*, while declining by 60% for *C. ascanius*. Because logging in planted forest at Kakamega was localized and presumably affected relatively small percentages of the home ranges of *C. ascanius* groups living in the planted forest [Cords, 1987], we cannot rule out the possibility that *C. ascanius* were simply avoiding the transect area where logging occurred in the two post-logging years, as has been reported for *Rhinopithecus roxellana* in China and *Gorilla gorilla* in Cameroon [Arnhem et al., 2008; Guo et al., 2008]. Nevertheless, whether their recorded drop in density was real or an artifact of changes in ranging patterns to avoid recently logged areas, *C. ascanius* appeared to be considerably less capable of coping with the immediate aftermath of logging of their habitat than *C. mitis* and *Colobus guereza* at Kakamega. Given its stability in density following logging and smaller disparity in density between natural and planted forest than exhibited by the guenon species, *C. guereza* appears to be the most ecologically-flexible of the diurnal primates at Kakamega, a result consistent with its reputation at Kibale, Uganda [Chapman et al., 2005; Oates, 1977; Skorupa, 1986].

Comparison of Different Group Density Estimation Techniques and Recommendations for Future Studies Involving Line Transect Censuses of Primates

The best practices for analyzing line-transect data for primates have been the subject of lively

debate in recent decades [Buckland et al., 2010a,b; Chapman et al., 1988; Fashing & Cords, 2000; Hassel-Finnegan et al., 2008; Marshall et al., 2008; Plumptre, 2000; Plumptre & Cox, 2006; Struhsaker, 1981; Whitesides et al., 1988]. Recently, Distance, a software program using mathematical models to estimate population density, has begun to gain prominence among primatologists [Buckland et al., 2010a; Pliosungnoen et al., 2010; Plumptre & Cox, 2006], although few efforts have been made to test density estimates generated by Distance in areas of known primate density [Ferrari et al., 2010; Hassel-Finnegan et al., 2008; Marshall et al., 2008]. Although we do not know the “true” population densities for Kakamega’s primates at present, in a previous study (1997–1998) in the natural forest at Kakamega we showed that the Whitesides method [Whitesides et al., 1988], another popular census data analysis technique, consistently generated density estimates very similar to “true” densities established through long-term study of home range size and overlap [Fashing & Cords, 2000].

In this study, using new (2006–2010) census datasets from both natural and planted forests at Kakamega, we compared density estimates generated by the Whitesides method [Whitesides et al., 1988] with those produced by a recently suggested modified version of the Distance method, which (like the Whitesides method) incorporates a measure of mean group spread into density calculations [Buckland et al., 2010a]. For the three diurnal primate species in planted and natural forest at our study site, the two techniques generated often markedly similar density results. While the overall consistency between the results produced by the Whitesides and Distance methods in our study is encouraging, we advocate further simultaneous testing of these techniques at other forested sites where “true” primate densities are known.

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REFERENCES

- Andrenaz M, Marshall A, Goossens B, van Schaik C, Sugardjito J, Gumal M, Wich S. 2008. *Pongo pygmaeus*. In: IUCN 2011 Red List of Threatened Species. Downloaded on 7 August 2011.
- Anderson J, Rowcliffe JM, Cowlishaw G. 2007. The Angola black-and-white colobus (*Colobus angolensis palliatus*) in Kenya: historical range contraction and current conservation status. *American Journal of Primatology* 69:664–680.
- Arnhem E, Dupain J, Vercauteren Drubbel R, Devos C, Vercauteren M. 2008. Selective logging, habitat quality and home range use by sympatric gorillas and chimpanzees: a case study from an active logging concession. *Folia Primatologica* 79:1–14.
- Barlow J, Gardner TA, Araujo IS, Ávila-Pires TC, Bonaldo AB, Costa JE, Esposito MC, Ferreira LV, Hawes J, Hernandez MIM et al. 2007a. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences* 104:18555–18560.
- Barlow J, Mestre LAM, Gardner TA, Peres CA. 2007b. The value of primary, secondary and plantation forests for Amazonian birds. *Biological Conservation* 136:212–231.
- Bleher B, Uster D, Bergsdorf T. 2006. Assessment of threat status and management effectiveness in Kakamega Forest, Kenya. *Biodiversity and Conservation* 15:1159–1177.
- Bonham KJ, Mesibov R, Bashford R. 2002. Diversity and abundance of some ground-dwelling invertebrates in plantation vs. native forests in Tasmania, Australia. *Forest Ecology and Management* 158:237–247.
- Bremer LL. 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and Conservation* 19:3893–3915.
- Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J. 2008. Plantation forests and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation* 17:925–951.
- Buckland S, Plumptre A, Thomas L, Rexstad E. 2010a. Design and analysis of line transect surveys for primates. *International Journal of Primatology* 31:833–847.
- Buckland S, Plumptre A, Thomas L, Rexstad E. 2010b. Line transect sampling of primates: can animal-to-observer distance methods work? *International Journal of Primatology* 31:485–499.
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L. 2001. *Introduction to distance sampling*. Oxford: Oxford University Press.
- Carnus J-M, Parrotta J, Brockerhoff E, Arbez M, Jactel H, Kremer A, Lamb D, O’Hara K, Walters B. 2006. Planted forests and biodiversity. *Journal of Forestry* 104:65–77.
- Carle J, Vuorinen P, Del Lungo A. 2002. Status and trends in global forest plantation development. *Forest Products Journal* 52:12–23.
- Chapman C, Fedigan LM, Chapman L. 1988. A comparison of transect methods of estimating population densities of Costa Rican primates. *Brenesia* 30:67–80.
- Chapman CA, Struhsaker TT, Lambert JE. 2005. Thirty years of research in Kibale National Park, Uganda, reveals a complex picture for conservation. *International Journal of Primatology* 26:539–555.
- Cords M. 1987. Mixed-species association of Cercopithecus monkeys in the Kakamega Forest, Kenya. University of California Publications in Zoology, Vol. 17. Berkeley: University of California Press.
- Cords M. in press. The thirty year blues: what we know and don’t know about life history, group size and group fission of blue monkeys in the Kakamega Forest, Kenya. In: Kappeler P, Watts D, editors. *Long-term studies of primates*. Berlin: Springer.

- Cords M, Chowdhury S. 2010. Life history of *Cercopithecus mitis stuhlmanni* in the Kakamega Forest, Kenya. *International Journal of Primatology* 31:433–455.
- Cords M, Rowell TE. 1986. Group fission in blue monkeys of the Kakamega Forest, Kenya. *Folia Primatologica* 46:70–82.
- Dela JDS. 2007. Seasonal food use strategies of *Semnopithecus vetulus nestor*, at Panadura and Piliyandala, Sri Lanka. *International Journal of Primatology* 28:607–626.
- Evans J, editor. 2009. *Planted forests: uses, impacts, and sustainability*. Rome: CAB International and FAO. 213p.
- Evans J, Turnbull JW. 2004. *Plantation forestry in the tropics*. Oxford: Oxford University Press.
- Fahy O, Gormally M. 1998. A comparison of plant and carabid beetle communities in an Irish oak woodland with a nearby conifer plantation and clearfelled site. *Forest Ecology and Management* 110:263–273.
- FAO. 2010. *Global forest resources assessment 2010*. FAO Forestry Paper No. 163, Rome.
- Farwig N, Sagita N, Bohning-Gaese K. 2008. Conservation value of forest plantations for bird communities in western Kenya. *Forest Ecology and Management* 255:3885–3892.
- Farwig N, Sajita N, Böhning-Gaese K. 2009. High seedling recruitment of indigenous tree species in forest plantations in Kakamega Forest, western Kenya. *Forest Ecology and Management* 257:143–150.
- Fashing PJ, Cords M. 2000. Diurnal primate densities and biomass in the Kakamega Forest: an evaluation of census methods and a comparison with other forests. *American Journal of Primatology* 50:139–152.
- Fashing PJ, Forrester A, Scully C, Cords M. 2004. Long-term tree population dynamics and their implications for the conservation of the Kakamega Forest, Kenya. *Biodiversity and Conservation* 13:753–771.
- Felton AM, Engström LM, Felton A, Knott CD. 2003. Orangutan population density, forest structure and fruit availability in hand-logged and unlogged peat swamp forests in West Kalimantan, Indonesia. *Biological Conservation* 114:91–101.
- Ferrari SF, Chagas RRD, Souza-Alves JP. 2010. Line transect surveying of arboreal monkeys: problems of group size and spread in a highly fragmented landscape. *American Journal of Primatology* 72:1100–1107.
- Ganzhorn JU. 1987. A possible role of plantations for primate conservation in Madagascar. *American Journal of Primatology* 12:205–215.
- Ganzhorn JU, Abraham JP. 1991. Possible role of plantations for lemur conservation in Madagascar: food for folivorous species. *Folia Primatologica* 56:171–176.
- Gillespie TR, Chapman CA, Greiner EC. 2005. Effects of logging on gastrointestinal parasite infections and infection risk in African primates. *Journal of Applied Ecology* 42:699–707.
- Guo S, Ji W, Li B, Li M. 2008. Response of a group of Sichuan snub-nosed monkeys to commercial logging in the Qinling Mountains, China. *Conservation Biology* 22:1055–1064.
- Hanya G, Zamma K, Hayashi S, Yoshihiro S, Tsuruya Y, Sugaya S, Kanaoka MM, Hayakawa S, Takahata Y. 2005. Comparisons of food availability and group density of Japanese macaques in primary, naturally regenerated, and plantation forests. *American Journal of Primatology* 66:245–262.
- Harvey PH, Martin RD, Clutton-Brock TH. 1987. Life histories in comparative perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham R, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 181–196.
- Hassel-Finnegan H, Borries C, Larney E, Umponjan M, Koenig A. 2008. How reliable are density estimates for diurnal primates? *International Journal of Primatology* 29:1175–1187.
- IUCN. 2010. *IUCN Red List of Threatened Species*. Version 2010.4. <www.iucnredlist.org>. Downloaded on 7 August 2011.
- Johns AD, Skorupa JP. 1987. Responses of rain-forest primates to habitat disturbance: a review. *International Journal of Primatology* 8:157–191.
- Kanowski J, Catterall CP, Wardell-Johnson GW. 2005. Consequences of broadscale timber plantations for biodiversity in cleared rainforest landscapes in tropical and subtropical Australia. *Forest Ecology and Management* 208:359–372.
- Lambin EF, Geist HJ, Lepers E. 2003. Dynamics of land-use and land-cover change in tropical regions. *Annual Review of Environment and Resources* 28:205–241.
- Lantschner MV, Rusch V, Peyrou C. 2008. Bird assemblages in pine plantations replacing native ecosystems in NW Patagonia. *Biodiversity and Conservation* 17:969–989.
- Lindenmayer DB. 2009. Forest wildlife management and conservation. *Annals of the New York Academy of Sciences* 1162:284–310.
- Mammides C, Cords M, Peters MK. 2009. Effects of habitat disturbance and food supply on population densities of three primate species in the Kakamega Forest, Kenya. *African Journal of Ecology* 47:87–96.
- Marshall AR, Lovett JC, White PCL. 2008. Selection of line-transect methods for estimating the density of group-living animals: lessons from the primates. *American Journal of Primatology* 70:452–462.
- Meijaard E, Albar G, Nardiyono, Rayadin Y, Ancrenaz M, Spehar S. 2010. Unexpected ecological resilience in Bornean orangutans and implications for pulp and paper plantation management. *PLoS One* 5:e12813.
- Merker S, Yustian I. 2008. Habitat use analysis of Dian's tarsier (*Tarsius diana*) in a mixed-species plantation in Sulawesi, Indonesia. *Primates* 49:161–164.
- Merker S, Yustian I, Muhlenberg M. 2005. Responding to forest degradation: altered habitat use by Dian's tarsier *Tarsius diana* in Sulawesi, Indonesia. *Oryx* 39:189–195.
- Miller E. 2010. *Mixed-species associations of blue and black-and-white colobus monkeys in the Kakamega Forest, Kenya* [M.A.]. New York: Columbia University. 65p.
- Mitani JC, Struhsaker TT, Lwanga JS. 2000. Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: implications for conservation and census methods. *International Journal of Primatology* 21:269–286.
- Mitchell N. 2004. *The exploitation and disturbance history of Kakamega Forest, western Kenya*. BIOTA East Report No. 1. Bielefeld: Bielefeld University.
- Mitchell N, Schaab G, Wagele JW. 2009. *Kakamega forest ecosystem: an introduction to the natural history and human context*. BIOTA East Africa Report No. 5. Karlsruhe: Karlsruhe University.
- Morrogh-Bernard H, Husson S, Page SE, Rieley JO. 2003. Population status of the Bornean orang-utan (*Pongo pygmaeus*) in the Sebangau peat swamp forest, Central Kalimantan, Indonesia. *Biological Conservation* 110:141–152.
- Nasi R, Koponen P, Poulsen J, Buitenzorg M, Rusmantoro W. 2008. Impact of landscape and corridor design on primates in a large-scale industrial tropical plantation landscape. *Biodiversity and Conservation* 17:1105–1126.
- Oates JF. 1977. The guereza and its food. In: Clutton-Brock TH, editor. *Primate ecology*. London: Academic Press. p 276–321.
- Oates JF. 1999. *Myth and reality in the rain forest: how conservation strategies are failing in West Africa*. Berkeley, CA: University of California Press.
- Oates JF, Whitesides GH, Davies AG, Waterman PG, Green SM, Dasilva GL, Mole S. 1990. Determinants of variation in tropical forest primate biomass: new evidence from West Africa. *Ecology* 71:328–343.
- Okali D, Eyog-Matig O. 2004. *Rain forest management for wood production in west and central Africa. Lessons learnt on sustainable forest management in Africa*. Nairobi: African Forest Research Network. p 79.

- Olupot W. 2000. Mass differences among male mangabey monkeys inhabiting logged and unlogged forest compartments. *Conservation Biology* 14:833–843.
- Pliosungnoen M, Gale G, Savini T. 2010. Density and microhabitat use of Bengal slow loris in primary forest and non-native plantation forest. *American Journal of Primatology* 72:1108–1117.
- Plough FH, Smith EM, Rhodes DH, Collazo A. 1987. The abundance of salamanders in forest stands with different histories of disturbance. *Forest Ecology and Management* 20:1–9.
- Plumptre AJ. 2000. Monitoring mammal populations with line transect techniques in African forests. *Journal of Applied Ecology* 37:356–368.
- Plumptre AJ, Cox D. 2006. Counting primates for conservation: primate surveys in Uganda. *Primates* 47:65–73.
- Plumptre AJ, Reynolds V. 1994. The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *Journal of Applied Ecology* 31:631–641.
- Rovero F, Struhsaker T, Marshall A, Rinne T, Pedersen U, Butynski T, Ehardt C, Mtui A. 2006. Abundance of diurnal primates in Mwanihana Forest, Udzungwa Mountains, Tanzania. *International Journal of Primatology* 27:675–697.
- Russon AE, Wich SA, Anrenaz M, Kanamori T, Knott CD, Kuze N, Morrogh-Bernard HC, Pratje P, Ramlee H, Rodman P et al. 2009. Geographic variation in orangutan diets. In: Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP, editors. *Orangutans: geographic variation in behavioral ecology and conservation*. Oxford: Oxford University Press. p 135–156.
- Skorupa JP. 1986. Responses of rainforest primates to selective logging in Kibale Forest, Uganda: a summary report. In: Benirschke K, editor. *Primates: the road to self-sustaining populations*. New York: Springer. p 57–70.
- Struhsaker TT. 1981. Census methods for estimating densities. In: Anonymous, editor. *Techniques for the study of primate population ecology*. Washington: National Academy Press. p 36–80.
- Struhsaker TT. 1997. *Ecology of an African Rain Forest: logging in Kibale and the conflict between conservation and exploitation*. Gainesville: University of Florida Press. 432p.
- Teelen S. 2007. Primate abundance along five transect lines at Ngogo, Kibale National Park, Uganda. *American Journal of Primatology* 69:1030–1044.
- Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL, Bishop JRB, Marques TA, Burnham KP. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* 47:5–14.
- Waltert M, Lien KF, Mühlenberg M. 2002. Further declines of threatened primates in the Korup Project Area, south-west Cameroon. *Oryx* 36:257–265.
- Whitesides GH, Oates JF, Green SM, Kluberanz RP. 1988. Estimating primate densities from transects in a West African rain forest: a comparison of techniques. *Journal of Animal Ecology* 57:345–367.