

The Long-term Impact of Timber Harvesting on the Resource Base of Chimpanzees in Kibale National Park, Uganda

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ABSTRACT

Commercial timber harvesting results in the loss of critical habitat for tropical forest fauna, and large-bodied frugivores (including chimpanzees and most other apes) may experience particularly detrimental effects. Few quantitative data, however, are available to evaluate the long-term impact of harvesting on chimpanzees and other apes. In particular, few data are available to compare population demographics and/or forest composition before and after timber harvesting at the same site. Utilizing detailed forestry department records of logging operations conducted in the late 1960s, present-day botanical surveys, and long-term data on the feeding ecology of chimpanzees in Kibale National Park (KNP), Uganda, I examined the impact that logging has had on KNP chimpanzee communities of known size and demography. Although some important chimpanzee food resources were harvested in high abundance during commercial logging operations, the overall impact on the most predominant dietary items (those making up roughly 75% of the chimpanzees' diet) and on presumably critical subsistence resources was limited. Furthermore, the low density of chimpanzees inhabiting the logged region of KNP is apparently not attributable to the impact of logging at the site: comparisons of resource densities at this 'low-chimpanzee-density' site with that of an unlogged and 'high-chimpanzee-density' KNP site did not differ when logging concessions at the low-chimpanzee-density site were excluded from the analysis. This study suggests that low-intensity logging can be compatible with the conservation of large-bodied frugivores, provided that dietary data are taken into account in forest management planning.

Key words: conservation; frugivore; logging; *Pan troglodytes*; subsistence resources.

COMMERCIAL TIMBER HARVESTING results in the loss of approximately 13 million ha of forest cover per year in the tropics, including considerable incidental and nonquantified structural damage (FAO 2005). A large body of research has been devoted to identifying the multi-scale behavioral and demographic responses of tropical forest animal populations to these disturbance processes (Johns 1983, Skorupa 1988, Plumptre & Reynolds 1994, Laurance *et al.* 2000, Peres 2001). Despite this intensive focus, few generalizations currently exist regarding the long-term impact of logging on tropical fauna.

Because of their slow intrinsic rates of population growth and diets linked closely to reproductive plant parts (primarily fruit), chimpanzees *Pan troglodytes* Blumenbach 1775 inhabiting tropical forests in equatorial Africa have been thought to be highly susceptible to the negative effects of even low-intensity selective logging (Johns & Skorupa 1987, Cowlshaw & Dunbar 2000). Although a number of studies examining the demographic responses of chimpanzee populations to timber harvesting present evidence in favor of this claim (Marchesi *et al.* 1995, White & Tutin 2001, Matthews & Matthews 2004) others are ambiguous or find no evidence of a negative influence (Plumptre & Reynolds 1994, Dupain *et al.* 2004, Arnhem *et al.* 2008). Chimpanzees thus present a useful case study for critically examining both the effects of logging on long-lived tropical fauna and the methods used in investigating such effects.

A common approach in many of these studies is to assess the potential impact of logging on the resource base of chimpanzees by

comparing the current structure and composition of the forest in botanical plots (or transects) placed within logged forest with that in plots (or transects) placed within unlogged regions of the same site (Hashimoto 1995, Matthews & Matthews 2004). A potential pitfall of such analysis is that, by comparing present-day logged regions to present-day unlogged regions, one implicitly assumes that the unlogged forest equates to a 'control' treatment (to be compared with the 'logging' treatment), and any structural or compositional differences found between treatments are likely a result of logging (Struhsaker 1997). In reality, it is probable that, particularly in highly diverse tropical biomes, the structure and composition of adjacent regions of forest differ naturally, independent of logging treatment, due to large edaphic variation across small spatial scales characteristic of such habitats (*e.g.*, Kibale National Park [KNP]: Chapman *et al.* 1997, Potts 2008; Jatun Sacha, Ecuador: DeVries *et al.* 1997; La Selva, Costa Rica: Clark *et al.* 1998; Gunung Palung National Park, Indonesia: Webb & Peart 2000). It is therefore imperative that studies comparing logged and unlogged regions to investigate logging effects additionally account for the extent of natural variation within undisturbed forest; however, this requires knowledge of the structure and composition of forestry concessions before the onset of logging. For studies conducted many years postlogging, such data are often unavailable. Understanding the extent of within-forest heterogeneity in the absence of logging can be useful in confirming whether logging or natural ecological variation is responsible for observed variation in primate density.

Furthermore, it is important that studies take into account the particular plant species being harvested during logging operations, as the extraction of certain taxa (*i.e.*, species filling important dietary roles for primary consumers) will likely impact the long-term viability of a consumer population, while the extraction of others

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may be essentially irrelevant for the population. In the case of chimpanzees, as well as in other frugivores, it is likely that species providing sufficient quantities of high-quality resources during times of relative fruit scarcity (roughly equivalent to 'fallback foods'; Lambert 2007, Marshall & Wrangham 2007) play critical roles in allowing individuals to maintain sufficient caloric intake during lean periods (also see Yamakoshi 1998, Peres 2000, Furuichi *et al.* 2001, Marshall & Leighton 2006, Potts 2008). Thus, extraction of plant species filling this particular dietary niche may affect chimpanzee populations to a greater extent than would the extraction of other plant species. The ability to take into account such species-specific information requires: (1) precise data on timber species and basal areas extracted and (2) detailed data on the feeding ecology of the animal species in question. The first set of data may be logistically difficult to obtain, whereas the second requires long-term observations of focal animals or repeated censuses of populations (both of which entail considerable time and effort).

KNP in southwestern Uganda is one of the few study locales in which all the requisite datasets described above are available for assessing the impact of logging on large-bodied apes. First, direct observations of chimpanzee behavior and ecology at two locations in KNP have yielded detailed and precise information on the diet of chimpanzees over the past 18 yr at one location (the Kanyawara study site) and 12 yr at another (the Ngogo study site). Second, Uganda Forestry Department records documented not only the total intensity of logging across several forestry concessions during mechanized logging operations (1966–1975) in KNP, but also the approximate species-specific off-take of known tree and liana species (in terms of basal area extracted and of percentage of total off-take; summarized in Table 2.1 in Skorupa 1988). Finally, the density of chimpanzees in KNP is unevenly apportioned among sites, and the two long-term study sites (Kanyawara and Ngogo) differ threefold in chimpanzee abundance and density (Potts 2008). The Kanyawara site is made up of relatively intact, unlogged forest adjacent to areas that were designated as forestry concessions in the 1960s (Struhsaker 1997). Mechanized harvesting took place at various intensities in these concession areas during the late 1960s (Skorupa 1988), but the site has not been commercially logged since. In contrast, the Ngogo site has never been subjected to commercial logging. Examination of ecological heterogeneity between similarly forested and unlogged regions of Kanyawara and Ngogo provides an opportunity to assess natural edaphic variation within KNP that may be influencing chimpanzee density (Potts *et al.* 2009). I include several comparisons here of the botanical characteristics among locations in KNP to elucidate the influences of logging on chimpanzees in the park: (1) heavily logged (forestry compartment K15) and lightly logged (compartment K14) vs. unlogged (compartment K30) regions of a site (Kanyawara) inhabited by a single community of chimpanzees; (2) a logged site (Kanyawara) currently supporting a low density of chimpanzees vs. an unlogged site (Ngogo) currently supporting an extremely high density of chimpanzees (see Potts *et al.* 2009 for detailed analysis); and (3) unlogged regions (compartment K30) of the low-chimpanzee-density site vs. the entire high-chimpanzee-density site. In making these comparisons, I consider only the impact of harvesting of

targeted trees on the resulting resource base of the forest. This methodology is unable to account for the effects of incidental damage to the forest resulting from mechanized logging operations that reportedly reduced basal area by up to 50 percent in some logging concessions in KNP (Skorupa 1988, Struhsaker 1997). Because such damage is indiscriminant, it is impossible, *post-hoc*, to assess its role in reducing the availability of particular tree species. With these limitations in mind, however, it is assumed here that plant species fulfilling important dietary niches for chimpanzees in KNP were uniformly affected by any incidental damage resulting from logging off-take. This assumption is supported by studies of incidental forest damage in Malaysia (Johns 1988), and implies that the proportional basal area representation of a given species, whether it is a targeted commercial timber species or not, will be relatively unchanged by incidental damage to a forest stand (Johns 1988).

METHODS

STUDY SITE.—KNP (766 km²) is located in southwestern Uganda near the foothills of the Ruwenzori Mountains (Skorupa 1988, Struhsaker 1997). The park consists of moist semi-deciduous and evergreen forest (57%), grassland (15%), woodland (4%), lakes and wetlands (2%), colonizing forest (19%), and plantations of exotic trees (1%; Chapman & Lambert 2000). There are distinct wet and dry seasons in KNP that are bimodal in distribution (Chapman *et al.* 1999). The biomass of the primate community in KNP is among the highest ever reported (Oates *et al.* 1990), and the density of chimpanzees is higher than at any other site in Uganda (Plumptre & Cox 2006) and among the highest known densities in Africa (Oates 2006). This study was conducted at the two forested KNP sites mentioned above—Kanyawara, the site of logging operations during the 1960s (though no commercial harvesting occurs today) and of currently low chimpanzee density, and Ngogo, a site unaffected by logging, located just 12 km from Kanyawara, and currently supporting an extremely high density of chimpanzees.

Kanyawara, the low-chimpanzee-density site, is in the northern sector of Kibale (Fig. 1) at an average altitude of *ca* 1500 m and is classified by foresters as *Parinari* forest (Skorupa 1988). Beginning in 1966 and ending by the early 1970s, areas within and adjacent to Kanyawara designated as forestry compartments were subjected to varying intensities of mechanized logging on a polycyclic scale (Kasene 1987, Skorupa 1988, Struhsaker 1997, Chapman & Lambert 2000). Kibale Forest has since received National Park status (in 1993) and mechanized logging has thus ceased at Kanyawara. The Kanyawara chimpanzee community most commonly uses forestry compartments K14, K15, and K30 (Emery Thompson *et al.* 2007). K14 (405 ha, or *ca* 39% of the area used by chimpanzees) was selectively harvested in 1969, resulting in an off-take of *ca* 5.1 stems/ha (Skorupa 1988). It is currently composed of late-stage regenerating forest with small patches of herbaceous vegetation. K15 (347 ha, or *ca* 33% of the area used by chimpanzees) was subjected to heavy logging between 1968 and 1969, resulting in clearing of approximately 7.4 stems/ha (Skorupa 1988), and is now dominated by a dense herbaceous layer interspersed with smaller mature forest patches. K30 (282 ha, or *ca* 27% of the area used by

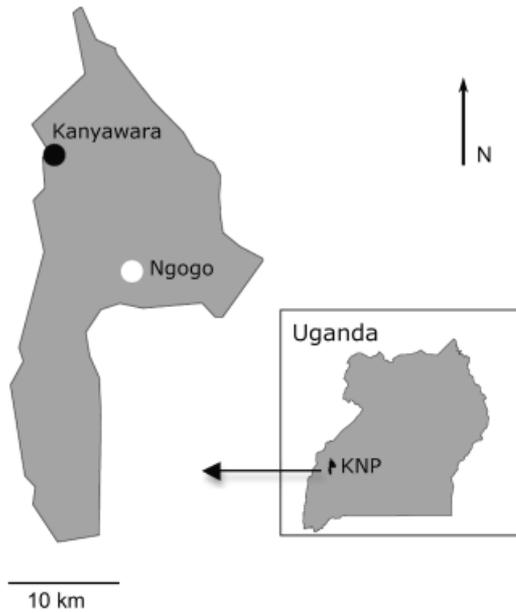


FIGURE 1. Map showing the location of Kibale National Park (KNP) in southwestern Uganda and, within KNP, the locations of the two study sites (Kanyawara and Ngogo).

chimpanzees) has never been commercially logged and is currently dominated by mature primary forest (Struhsaker 1997). Although chimpanzees use each of these compartments to varying degrees, the majority of individuals in the community currently ranges predominantly in lightly logged K14 and unlogged K30 (though a distinct 'cluster' of females ranges mostly in heavily logged K15; Emery Thompson *et al.* 2007).

Ngogo, the high-chimpanzee-density site, is about 12 km south-east of the low-chimpanzee-density site (Fig. 1) and is at a slightly lower elevation (1350 m). Floristic composition there differs distinctly from that at the low-chimpanzee-density site (Chapman *et al.* 1997), and is more consistent with lowland than montane forest. The dominant timber species at the low-chimpanzee-density site (*Parinari excelsa*) is still found at Ngogo, but the forest is more mixed. No species is dominant, although *Chrysophyllum albidum*, *Celtis* spp., *Prerygota mildbraedii*, and *Piptadeniastrum africanum* (some of which are extremely rare at the low-chimpanzee-density site; Chapman *et al.* 1997, Potts 2008) are co-dominant in much of the area (Chapman & Lambert 2000). In contrast to the low-chimpanzee-density site, the forest at the high-chimpanzee-density site has never been commercially logged (Struhsaker 1997), but the site has a history of human habitation, perhaps as recently as the 1930s (Wing & Buss 1970, Lwanga 2006a). As a result, the site is currently composed of heterogeneous forest types, including large tracts of old growth stands adjacent to colonizing forests (that were grasslands until 1955; Lwanga 2006a), swamp forest and, on hilltops, anthropogenic grasslands maintained by burning (Lwanga *et al.* 2000, Lwanga 2003).

Basuta (1988) was the first to intensively study chimpanzees at Kanyawara between 1983 and 1985. Wrangham and colleagues

began to habituate the community in the late 1980s and early 1990s, and now conduct all-day follows of focal chimpanzees (Wrangham *et al.* 1991, Conklin-Brittain *et al.* 1998, Muller & Wrangham 2004, Emery Thompson *et al.* 2007). Community size at Kanyawara has varied between 40 and 50 since the onset of habituation. The community had 11 adult males, 1 subadult male, 15 adult females, 3 nulliparous females, 8 juveniles, and 13 infants during my study. The density of chimpanzees at Kanyawara was approximately 1.5 individuals/km² at the time of this study (Emery Thompson *et al.* 2007).

Ghiglieri (1984) conducted the first study of the chimpanzee community at Ngogo in the late 1970s and early 1980s. Wrangham *et al.* (1991) briefly studied chimpanzees there in the late 1980s and 1990, but intensive research and habituation at Ngogo (by D. P. Watts and J. C. Mitani) did not commence until 1995. The community has been continuously observed since (Watts 1998; Mitani & Watts 1999, 2005; Watts & Mitani 2001; Watts *et al.* 2006). It is the largest chimpanzee community ever observed, with > 150 members. At the time of this study, 23–26 adult males, 15 adolescent males, at least 44 adult females, 15 adolescent females, 17 juveniles, and 34 infants resided within the community. The density of chimpanzees at Ngogo was *ca* 5.1 individuals/km² at the time of this study.

ASSESSING THE IMPACT OF LOGGING ON RESOURCES IMPORTANT TO CHIMPANZEES.—To establish the resource base of chimpanzees at the two sites, I used long-term data from each site (*ca* 15 yr of published data from Kanyawara and 10 yr of unpublished data from Ngogo; Basuta 1988; Conklin-Brittain *et al.* 1998, 2006; Wrangham *et al.* 1998; Potts 2008; D. P. Watts, J. S. Lwanga, & K. B. Potts, unpubl. data). From these datasets I generated a list of 18 tree species at each site that have contributed to > 1 percent of chimpanzee feeding records since the onset of research at the sites (only including those utilized for fruit by chimpanzees, as fruit constitutes > 74 percent of feeding time for KNP chimpanzees; Wrangham *et al.* 1998). I categorized each plant species into one of three categories: high-food-abundance (HFA); synchronous-low-food-abundance (sLFA); or asynchronous-low-food-abundance (aLFA), based on its tendency to bear fruit during HFA or low-food-abundance (LFA) months and, among LFA foods, on its degree of fruiting synchrony ('s' = synchronous, 'a' = asynchronous; see Potts *et al.* 2009 for details). Briefly, HFA foods are those for which > 30 percent of all fruiting events occurred during HFA months (with high and low fruit abundance months defined as months with fruit abundance indices above the 75th percentile or below the 25th percentile, respectively, based on 82 mo of phenology data from each site; details are given in Potts *et al.* 2009). sLFA foods are those for which > 20 percent of fruiting events took place in LFA months, and that fruit synchronously among individuals. aLFA foods are those for which > 20 percent of fruiting events took place in LFA months, and that have low fruiting synchrony. For a given species exhibiting completely random fruiting, 25 percent of all fruiting events should fall in HFA months and 25 percent in LFA months, based on my definition of HFA and LFA months given above. By definition, however, more species should fruit, and at a higher

intensity, in HFA months than in LFA months. It is for this reason that I considered the cutoff for inclusion as an HFA food to be 30 percent of fruiting events during HFA months, whereas only 20 percent of fruiting events occurring during LFA months warranted inclusion as an LFA food. In each analysis, I also included among-site comparisons of the basal area of all major fruit-providing species (18 total; see Potts 2008 for details) and of the top seven most common items used for fruit by chimpanzees (*i.e.*, those accounting for 78–94% of time spent eating fruit per month, or 60–80% of total feeding time based on long-term monthly feeding scan data Wrangham *et al.* 1996) as a general measure of the impact of logging on the resource base of chimpanzees.

I determined the density and basal area of these plant species by enumerating and measuring woody plants in 104 botanical plots covering an equal area at both the Kanyawara and Ngogo sites (52 plots/site, 13 ha sampled/site; see Potts 2008 for details). I constructed each plot along a 50 m midline and used nested strip widths of 50, 25, and 5 m to measure stems of different size classes and growth forms: trees and free-standing figs with diameters at breast height (dbh) > 80 cm, and strangler figs with dbh ≥ 10 cm, in large plots (50 × 50 m); trees and figs of 30 < dbh < 80 cm in intermediate-sized plots (25 × 50 m); and trees and figs 10 < dbh < 30 cm in small (5 × 50 m) plots. Plots were placed using a stratified random methodology such that the representation of a given habitat type in botanical sampling was directly proportional to its representation in the habitat as a whole (Potts 2008).

I used timber off-take records (Uganda National Forest Authority, summarized in Table 2.1 in Skorupa 1988) to assess the impact of various intensities of logging on the resource base as a whole, and on individual resource classes, at Kanyawara. Particular emphasis was placed on the availability of plant species with high inter-individual fruiting synchrony that tended to provide fruit during periods of low habitat-wide fruit availability (sLFA species). Previous research comparing the flora at these two sites (Potts 2008, Potts *et al.* 2009) suggested that sLFA taxa may be particularly important in influencing chimpanzee population ecology and may be prominent indicators of habitat quality (see also Marshall & Wrangham 2007). As mentioned above, the presence of these taxa in high abundance results in temporal reliability of the resource base and, because estrous cycling and pregnancy in chimpanzees are profoundly impacted by caloric shortfalls (Emery Thompson & Wrangham 2008), can greatly influence long-term population dynamics. Therefore, sLFA stem abundance and basal area are likely useful indicators of habitat carrying capacity for chimpanzees. If logging operations significantly impacted stems of sLFA taxa, this would provide strong support for the notion that long-term chimpanzee conservation may be incompatible with such activities (Potts 2008 discusses the potential role of aLFA and HFA species in influencing chimpanzee populations). Conversely, if sLFA taxa were not greatly impacted by logging, it would suggest that the threefold difference in chimpanzee density between the Ngogo and Kanyawara sites is not primarily due to the effects of mechanized logging at Kanyawara, but rather is due to natural edaphic variation within Kibale. This would imply, in turn, that logging may be compatible with chimpanzee conservation, provided it occurs in areas with a

relatively low carrying capacity for chimpanzees while sparing higher density populations or subpopulations.

DATA ANALYSIS.—I performed three sets of analyses. First, I assessed the extent to which logging reduced the basal areas of HFA, aLFA, and sLFA resources at the Kanyawara (low-chimpanzee-density) site as a whole. I then compared the current basal areas of these same resource classes across forestry compartments K14 (lightly logged), K15 (heavily logged), K30 (unlogged) at Kanyawara. Finally, I compared the basal area of resources at Ngogo (the unlogged KNP site) with that at: (1) Kanyawara as a whole, including both unlogged and logged forest (see Potts *et al.* 2009); and (2) K30, the unlogged region of the Kanyawara site. If floristic differences between Kanyawara (unlogged and logged compartments considered together) and Ngogo (described in Potts 2008, Potts *et al.* 2009) hold when Ngogo is compared only with the unlogged forest at Kanyawara (K30), this would suggest that these differences represent natural trends, separate from any possible influences of logging at Kanyawara. Furthermore, this would imply that the threefold difference in chimpanzee density between the Ngogo and Kanyawara sites is not primarily due to the effects of mechanized logging at Kanyawara. As mentioned above, particular emphasis was placed on spatial variation in sLFA food abundance as an indicator of variability in chimpanzee carrying capacity.

I used nonparametric Kruskal–Wallis H tests to evaluate differences in resource basal areas among Kanyawara forestry compartments (and *post-hoc* Mann–Whitney U -tests to determine pairwise differences between compartments), and Mann–Whitney U -tests to evaluate differences between the Ngogo site and: (1) Kanyawara compartment K30 and (2) Kanyawara as a whole. H' (rather than H) and Z (rather than U) values are reported for all Kruskal–Wallis and Mann–Whitney U -tests, respectively, to account for ties among sampling units (there were several botanical plots in which the basal area of a particular resource class was zero, thus there were relatively many ‘tied’ sampling units) and to account for a relatively large number of sampling units ($N = 52$ botanical plots at both Kanyawara and Ngogo). Significance was placed at $P < 0.05$ for all tests.

RESULTS

WHICH RESOURCE GROUPS WERE NEGATIVELY IMPACTED BY LOGGING AT KANYAWARA?—Although timber extraction considerably affected the basal area of the top 18 species providing fruit for chimpanzees at the Kanyawara site, in particular in heavily logged K15 compartment (*ca* 30% of all K15 off-take by volume), this effect was disproportionately experienced by those food species *not* among the top seven dietary species (Tables 1 and S1). Among taxa included in the chimpanzee resource base, timber extraction was focused on *Aningeria (Pouteria) altissima* and *Celtis africana* (Table S1), both of which were among the most heavily felled species, but neither of which is considered a major (top seven) food species. Also, despite the noted extraction intensity of these species at Kanyawara, this site currently supports a 6 × and 8 × greater basal area/ha of reproductive-sized *A. altissima* and *C. africana*, respectively, than the

other KNP site, Ngogo (Potts 2008), which is inhabited by a chimpanzee community that is triple the size of that at Kanyawara, and which was not subjected to logging.

HOW DID LOGGING IMPACT sLFA FOOD SPECIES AT KANYAWARA?—As a class, sLFA taxa at Kanyawara were not heavily subjected to extraction (Tables 1 and S1), though *C. africana* accounted for 9.5 percent of all K14 timber, by volume. Despite the particularly heavy extraction of this species, it is presently among the most abundant of all species at Kanyawara (in terms of basal area) and, as noted above, it is not nearly as prominent in the diet as other sources (Emery Thompson & Wrangham 2008).

HOW DO UNLOGGED COMPARTMENTS OF THE LOW-CHIMPANZEE-DENSITY SITE COMPARE WITH UNLOGGED FOREST AT THE HIGH-CHIMPANZEE-DENSITY SITE?—Table 2 displays the results of comparisons of the basal areas of each of the resource classes (as well as each broken down into separate size/growth form components) between Ngogo

(unlogged, high-chimpanzee-density site) and K30 (unlogged compartment of Kanyawara, the low-chimpanzee-density site). It is also noted whether or not the results of the inter-site comparisons change when K30 is substituted for Kanyawara as a whole (see Potts *et al.* 2009 for comprehensive summaries of Ngogo–Kanyawara comparisons).

In total, the results of 54 percent (13/24) of comparisons differed between the two sets of analyses. Most notably, the significantly higher basal area/ha of all chimpanzee food species ($Z = -0.621$, $P > 0.05$) and of the top seven food species ($Z = -1.31$, $P > 0.05$) found at Ngogo when compared with all Kanyawara regions disappear when Ngogo is compared only with K30. Additionally, on a per hectare basis, K30 supports a higher basal area of HFA stems than does Ngogo ($Z = -2.67$, $P = 0.008$). When comparing K30 (rather than all of Kanyawara) to Ngogo, the only resource class that does not appear to influence the results of any of the comparative analyses is sLFA foods (the basal area/ha of sLFA was higher at Ngogo than at K30; $Z = -4.20$, $P < 0.001$; Table 2).

TABLE 1. Comparison of basal areas of resource classes across unlogged (K30), lightly logged (K14), and heavily logged (K15) forest at the Kanyawara site, and total estimated off-take from each forestry compartment (from Skorupa 1988). Resource classes differing significantly in basal areas across forestry compartments (based on Kruskal–Wallis H tests) are indicated in bold (and H' values are given). Pairwise differences between forestry compartments, based on Mann–Whitney's U-tests, are noted (e.g., '> K15' in the K30 column indicates that K30 had a higher basal area of the resource class in question than did K15). Cells with '-' as their contents indicate a lack of significant difference among compartments in basal area of the resource class in question.

Resource class	K30 (unlogged)	K14 (lightly logged)	K15 (heavily logged)	K14 off-take	K15 off-take
All species providing fruits for chimpanzees					
Large trees and strangler figs (H' = 6.07)	> K15	NS (= K15, K30)	< K30	2.03 m ³ /ha	6.22 m ³ /ha
Intermediate-sized stems		–		(0.72 stems/ha)	(2.21 stems/ha)
Small stems		–			
Overall		–			
Top seven food species					
Large trees and strangler figs (H' = 8.57)	> K15	> K15	< K30, K14	0.17 m ³ /ha	0.01 m ³ /ha
Intermediate-sized stems		–		(0.06 stems/ha)	(0.003 stems/ha)
Small stems		–			
Overall (H' = 12.67)	> K15	> K15	< K30, K14		
High-food-abundance foods (HFA)					
Large trees and strangler figs (H' = 10.28)	> K14, K15	< K30	< K30	0.62 m ³ /ha	6.05 m ³ /ha
Intermediate-sized stems		–		(0.22 stems/ha)	(2.15 stems/ha)
Small stems (H' = 9.02)	> K15	> K15	< K30, K14		
Overall		–			
Synchronous-low-food-abundance foods (sLFA)					
Large trees and strangler figs		–		1.37 m ³ /ha	0.17 m ³ /ha
Intermediate-sized stems		–		(0.50 stems/ha)	(0.06 stems/ha)
Small stems		–			
Overall		–			
Asynchronous-low-food-abundance foods (aLFA)					
Large trees and strangler figs		–		0.04 m ³ /ha	0.00 m ³ /ha
Intermediate-sized stems		–		(0.014 stems/ha)	(0.00 stems/ha)
Small stems		–			
Overall		–			

TABLE 2. Display of Mann–Whitney's U-tests comparing the basal areas of different resource classes between Ngogo and K30 (unlogged forestry compartment at Kanyawara). For significant inter-site differences, the direction of the difference is noted (e.g., Ngogo > K30) and Z scores and P values are given. It is also indicated whether or not these comparisons yield different results from those comparing Ngogo and Kanyawara as a whole (see Potts 2008 for full summaries of comparative analyses). Cells with '–' as their contents indicate a lack of significant differences between K30 and Ngogo for the resource class in question.

Resource class	Differences in basal area between K30 (unlogged region of Kanyawara) and Ngogo	Different result from comparison of Ngogo vs. all of Kanyawara (logged and unlogged regions)?
All species providing fruit for chimpanzees		
Large trees and strangler figs	–	Yes
Intermediate-sized stems	–	No
Small stems	–	Yes
Overall	–	Yes
Top seven food species		
Large trees and strangler figs	–	Yes
Intermediate-sized stems	Ngogo > K30 ($Z = -2.720$, $P = 0.006$)	No
Small stems	Ngogo > K30 ($Z = -2.48$, $P = 0.012$)	No
Overall	–	Yes
High-food-abundance foods (HFA)		
Large trees and strangler figs	K30 > Ngogo ($Z = -2.52$, $P = 0.006$)	Yes
Intermediate-sized stems	K30 > Ngogo ($Z = -2.24$, $P = 0.024$)	No
Small stems	–	Yes
Overall	K30 > Ngogo ($Z = -2.67$, $P = 0.008$)	Yes
Synchronous low-food-abundance foods (sLFA)		
Large trees and strangler figs	Ngogo > K30 ($Z = -2.79$, $P = 0.006$)	No
Intermediate-sized stems	Ngogo > K30 ($Z = -3.22$, $P = 0.001$)	No
Small stems	Ngogo > K30 ($Z = -2.13$, $P = 0.031$)	No
Overall	Ngogo > K30 ($Z = -4.30$, $P = 0.000$)	No
Asynchronous low-food-abundance foods (aLFA)		
Large trees and strangler figs	–	No
Intermediate-sized stems	–	Yes
Small stems	–	Yes
Overall	–	Yes
All trees/figs (food and non-food)		
Large trees and strangler figs	–	No
Intermediate-sized stems	–	No
Small stems	–	Yes
Overall	–	Yes

DISCUSSION

Although the harvesting regime of the 1960s in KNP resulted in a considerable, pervasive alteration of the structure and composition of the forest (Table 1; cf. Skorupa 1988, Chapman & Chapman 1997, Struhsaker 1997) with important consequences for various animal species (e.g., several timber species were important dietary items of red colobus monkeys; Chapman & Chapman 1999), this alteration appears to have had a limited impact on the resource base of chimpanzees. This is based on the fact that the most critical resources for these animals (both the most preponderant dietary items and the most critical 'subsistence' [sLFA] items) were either spared from the heaviest extraction or remained at unusually high densities

regardless of extraction. Also, the only resource class in which comparing unlogged compartment K30, rather than all of Kanyawara, with unlogged Ngogo did not change the results of any of the comparative analyses is sLFA foods (Table 2). The clear differences noted between Ngogo and Kanyawara in the availability of sLFA species (Potts *et al.* 2009), a resource class of critical importance for large-bodied frugivores (also see Marshall & Leighton 2006) and perhaps a key indicator of habitat-specific carrying capacity (Marshall & Leighton 2006), therefore likely represents a natural phenomenon differentiating the two sites. Thus my data suggest that natural heterogeneity within KNP has endowed particular sites in the forest with much higher habitat suitability measures for chimpanzees than others, and that these areas are inherently capable of

supporting a greater biomass of chimpanzees than others, independent of logging history.

The chimpanzee community size at Kanyawara has remained essentially stable since the onset of habituation of the group (in the late 1980s), especially in comparison with numerous other chimpanzee populations (Hill *et al.* 2001). Although female interbirth intervals are relatively long at Kanyawara (Wrangham *et al.* 1996), infrequent birthing events appear to be compensated for by generally high survivorship. It is possible that the harvesting regime of the 1960s resulted in an immediate decline in chimpanzee abundance and/or density at Kanyawara. Previous research from West Africa suggests that even low-intensity logging operations can displace entire communities of chimpanzees from an established home range (White & Tutin 2001), and resulting local reductions in density can persist up to 15 yr postlogging (Stokes *et al.* 2010). It is not unlikely that a similar, immediate reduction in chimpanzee density occurred following logging in KNP. Even if this were the case, however, the stability of the community over the past two decades suggests that logging operations apparently did not critically reduce the long-term viability of the community. It should be noted that these findings do not address the potential impact of logging on Kanyawara chimpanzees at a finer scale than the community range. Indeed, previous research from this site suggests that females with core areas in heavily logged K15 had less access to preferred food sources, reduced ovarian hormone production, longer interbirth intervals, and higher infant mortality rates than did females with core areas in lightly logged K14 and unlogged K30 (Emery Thompson *et al.* 2007). Within-community variance in fitness measures in relation to logging certainly deserves further attention, but was outside the scope of this study. Furthermore, while I have described differences between logged and unlogged forest in resource classes that I assumed to play the most critical ecological roles for chimpanzees in KNP and to most closely influence population dynamics, there are likely other potentially important resource classes that I have omitted in these analyses. Similarly, I have focused here on basal area differences across sites in particular resource classes, but several studies attest to the importance of both quantity and quality of resources in influencing population density of frugivores. For example, Rode *et al.* (2006) found that the population density of frugivorous redtail monkeys (*Cercopithecus ascanius*) in KNP was most closely related to habitat-specific concentrations of minerals, such as copper and sodium, in foods available across sites. Thus, the findings of the current study should be considered together with data on the nutritional ecology of chimpanzees at Kanyawara and Ngogo (Wrangham *et al.* 1998, Potts 2008). Despite these and other methodological limitations (*e.g.*, several important food species for Kanyawara chimpanzees grow as strangler figs, and thus were likely impacted by the extraction of large host trees, which may or may not have been included as chimpanzee food species in the analyses above), this study nonetheless suggests that commercial timber harvesting has had relatively little influence on the critical components of the resource base of chimpanzees at Kanyawara.

This is a surprising finding, in light of similar studies of the effects of logging on other large-bodied frugivorous taxa, as well as on other chimpanzee populations. Although there is evidence that

certain harvesting regimes are compatible with the long-term conservation of robust frugivorous vertebrate populations (*e.g.*, frugivorous mammals and birds in Tekam Forest Reserve, peninsular Malaysia, and the Ulu Segama Forest Reserve, Malaysian Borneo: Johns 1992; cercopithecine primates in Budongo Forest Reserve, Uganda: Plumptre & Reynolds 1994), a large number of studies have found logging effects in tropical forests to be detrimental to large-bodied vertebrates, and to frugivorous primates, in particular (see Johns & Skorupa 1987, Cowlshaw & Dunbar 2000). This is especially true in the case of primates inhabiting logging concessions in Central and West equatorial Africa (*e.g.*, Korup Project Area: Waltert *et al.* 2002; Campo and Ma'an Forests, Cameroon: Matthews & Matthews 2004; but see Arnhem *et al.* 2008).

One potential explanation for the relatively limited effect of logging on KNP chimpanzees is that, unlike many other large-bodied frugivore populations subjected to habitat disturbance, the population at KNP is, and has historically been, largely unaffected by hunting pressures (with the exception of areas far to the south of both Ngogo and Kanyawara; Struhsaker 1997, Carter *et al.* 2008). Although limited poaching does occur at both Ngogo and Kanyawara (based on the recovery of snares and, occasionally, poached carcasses; Lwanga 2006b, K. B. Potts, pers. obs.), chimpanzees are not often the target species. As in several other African moist forests (Fa & Brown 2009), ungulates are the primary target of poachers (Lwanga 2006b), and wire traps set for duikers occasionally ensnare chimpanzees, but rarely are the resulting wounds fatal. The local Batoro and Bakiga populations surrounding KNP do not intensively hunt primates and largely avoid bushmeat consumption (Struhsaker 1997). The role of hunting in magnifying the effects of logging on large-bodied vertebrates is likely an important component in explaining the relative resiliency of the Kanyawara chimpanzee community to commercial logging. Marshall *et al.* (2006) found that, contrary to similar studies (*e.g.*, Felton *et al.* 2003), logged forests in East Kalimantan supported relatively high densities of orangutans (*Pongo pygmaeus*). Forests located near villages known to hunt orangutans, however, supported relatively low densities of orangutans (Felton *et al.* 2003). Similarly, Peres (2001) found that the presence of subsistence hunting considerably reduced the ability of large-bodied vertebrate assemblages (including mammals and birds) to persist in Amazonian forest fragments, largely independent of the size of the fragment. Studies from Central and West Africa similarly suggest that low-intensity logging *per se* does not drive frugivorous primate populations to local extinction, but is only particularly detrimental where hunting and bushmeat consumption also exist (Matthews & Matthews 2004, Poulsen *et al.* 2009). Thus a key factor in determining the long-term success of large-bodied frugivore populations inhabiting logged regions may be the extent to which hunting pressure exacerbates pressures from reduced food supplies, fragmentation, etc.

These findings have important implications for the construction of forest management scenarios throughout the rapidly diminishing forested belt of equatorial Africa. When available, knowledge of the chimpanzee resource base and, in particular, information regarding species utilized for fruit during times of low overall food abundance, should be incorporated into such plans if commercial

harvesting is to be compatible with the long-term survival of chimpanzee populations. Sufficiently detailed data on chimpanzee diets, however, are scarce outside of sites of long-term (> 5 yr) research and monitoring (e.g., Goodall 1986, Wrangham *et al.* 1998, Newton-Fisher 1999). Nonetheless, relevant baseline feeding ecology data are obtainable via indirect methods, such as macroscopic analysis of feeding remains and feces (Hohmann *et al.* 2006). Such rapidly assessed information will undoubtedly prove indispensable in the formulation of future management plans aimed at producing treatments that are compatible with chimpanzee conservation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *The basal areas, classifications, and estimated basal area offtake per compartment of the top 18 fruit-providing species for chimpanzees at Kanyawara.*

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