

RESEARCH ARTICLE

Chimpanzee-Red Colobus Encounter Rates Show a Red Colobus Population Decline Associated With Predation by Chimpanzees at Ngogo

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Chimpanzees (*Pan troglodytes*) hunt various primates, but concentrate on red colobus monkeys (*Piliocolobus spp.*) wherever the two species are sympatric. The extraordinarily large Ngogo chimpanzee community in Kibale National Park, Uganda, preys heavily on the local population of red colobus (*P. tephrosceles*). Census data showed a steep decline in this population in the center of the chimpanzees' home range between 1975 and 2007 [Lwanga et al., 2011; Teelen, 2007b]. Given no obvious change in food availability, predation by chimpanzees was the most likely cause [*ibid.*; Teelen, 2008]. However, census data from other parts of the home range raised the possibility that the decline was restricted to this central area [Teelen, 2007a]. We present data from 1998 to 2012 on the rate of encounters between chimpanzees and red colobus that provide a chimpanzee-centered estimate of red colobus density, thus of predation opportunities, throughout the home range. These corroborate census data by showing a long-term decline in encounters near the center. They also show that encounters become relatively more common at increasing distances from the center, but encounter rates have decreased even in peripheral areas and, by implication, the red colobus population has declined throughout the study area. These data corroborate Teelen's [2008] conclusion that chimpanzee predation on red colobus during the 1990s and early 2000s was unsustainable. Hunting rates and prey offtake rates have also declined markedly; whether this will allow the red colobus population to recover is unknown. In contrast, rates at which chimpanzees encountered redbellied monkeys (*Cercopithecus ascanius*) and grey-cheeked mangabeys (*Lophocebus albigena*) did not decrease. Neither did they increase, however, contrary to long-term census data from the center of the study area [Lwanga et al., 2011]. *Am. J. Primatol.* 75:927–937, 2013. © 2013 Wiley Periodicals, Inc.

Key words: chimpanzees; red colobus; predation; hunting

INTRODUCTION

Much direct and indirect evidence [reviewed in Fichtel, 2012; Miller & Treves, 2007] highlights the importance of predation as a selective force on primate morphology and behavior and supports the hypotheses that the anti-predation benefits of grouping are the main reason why most diurnal primates form permanent, stable social groups [van Schaik, 1983] and that predation helps to explain the unusually slow life histories of most primates [Charnov & Berrigan, 1993; Jones, 2011]. Many studies of primates and predators have provided quantitative data on the intensity and effects of predation. For example, predation by fossa (*Cryptoprocta ferox*) is the main source of mortality for sifakas (*Propithecus verreauxi*) at Kirindy [Kappeler & Fichtel, 2012], while predation by carnivores and crocodiles is the main cause of mortality among female chacma baboons (*Papio ursinus*) at Moremi [Cheney & Seyfarth, 2007]. At Tai, radio-collaring leopards confirmed that they are major predators on

eight monkey species [Zuhnerbuhler and Jenny, 2002], while analysis of faunal remains collected at raptor nests there and at Ngogo yielded information

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on prey choice and predation rates [Mitani et al., 2001; Schultz et al., 2004].

Chimpanzees (*Pan troglodytes*) hunt a range of vertebrate species, especially other nonhuman primates. Because they and their primate prey can be habituated, research on predation by chimpanzees is valuable for assessing how predation affects prey behavior [Boesch, 1994; Stanford, 1998] and for investigating hunting strategies [Boesch & Boesch, 1989; Gilby et al., 2008; Watts & Mitani, 2002a]. This particularly applies to predation on red colobus monkeys (*Piliocolobus spp.*), the main prey of chimpanzees wherever the two are sympatric [Gilby & Connor, 2010]. For example, red colobus regularly participate in polyspecific associations with cercopithecids at Tai, Gombe, and Ngogo that benefit some participants [e.g., Diana monkeys (*Cercopithecus diana*) at Tai: Noë & Bshary, 1997; redbtail monkeys (*C. ascanius*) at Ngogo: Teelen, 2007a] by providing better ability to detect or deter chimpanzees and/or through dilution effects. However, red colobus apparently do not gain such benefits at Gombe [Stanford, 1998] or Ngogo [Teelen, 2007a], nor do they gain them at Tai despite primary responsibility for initiating associations [Boesch & Boesch-Achermann, 2000; Noë & Bshary, 1997]. Alternatively, red colobus may cease to call and/or move to safer positions when they hear chimpanzees outside of visual range; this should reduce the probability of detection or pursuit [Noë & Bshary, 1997; Teelen, 2005]. In turn, large chimpanzee parties with many males are more likely to pursue red colobus on encounter than are smaller parties with fewer males [Mitani & Watts, 2001], and in at least some habitats, chimpanzees hunt red colobus more often when fruit is abundant than when it is scarce [Gilby & Wrangham, 2007; Watts & Mitani, 2002a].

Chimpanzees also provide opportunities to assess how predation affects prey population dynamics, particularly for red colobus. For example, Stanford [1998] calculated that chimpanzee predation accounted for over 50% of red colobus infant mortality at Gombe during a 5-year period and that heavy predation on juveniles helped to explain why only 20% of red colobus females survived to maturity. Stanford [1995] also found that red colobus groups with home ranges in areas where adjacent chimpanzee territories overlapped were larger than those with home ranges entirely within one territory, presumably because the risk of intra-specific aggression makes chimpanzees reluctant to hunt in overlap areas.

Long-term research on chimpanzee behavioral ecology at Ngogo, in Kibale National Park, Uganda, has provided extensive data on hunting and predation [Mitani & Watts, 1999, 2001, 2005; Watts & Mitani, 2002a,b; Watts, 2012]. The Ngogo chimpanzee community is extraordinarily large: as of March, 2013, it had at least 190 members, including 33 adult

males. The frequency of red colobus hunts is not unusually high, but the chimpanzees kill prey in a much higher percentage of hunts than at Tai, Gombe, Mahale, or Kanyawara and make more than twice as many kills per successful hunt [Gilby & Wrangham, 2007; Mitani & Watts, 1999, 2001; Watts & Mitani, 2002a,b]. Teelen's [2005, 2007a,b, 2008] research on red colobus [*P. tephrosceles*] at Ngogo showed many effects of chimpanzees on the monkeys' behavior, including those noted above. She also used demographic and life history data to model the probability that the local red colobus population would persist for 100 years with and without chimpanzee predation. The probability was 100% without predation, but all simulations with predation levels documented in 1995–2002 led to local extinction unless hunting stopped when the population decreased to some threshold value, and extinction probabilities were high even with threshold effects [Teelen, 2008].

Teelen [2007b] also conducted censuses that showed a considerable decline in the density of red colobus groups along a long-used Ngogo census route in the center of the study area compared to earlier census results. Lwanga et al. [2011] extended this perspective by analyzing all data collected during 380 censuses along this route over 19 years of fieldwork between 1975 and 2007. They found that the mean number of red colobus groups encountered per hour decreased by nearly 90% and that the sighting rate declined consistently during most of this interval, although it reached an asymptote in 2003. In contrast, encounter rates with grey-cheeked mangabeys (*Lophocebus albigena*) and redbtail monkeys (*C. ascanius*)—the two most abundant primate species at Ngogo—increased significantly. They agreed with Teelen [2007b, 2008] that chimpanzee predation most likely caused the decline in red colobus density, and argued that the redbtail population increase was due to regeneration of young forest containing abundant food resources from anthropogenic grassland in areas protected from fire [cf. Lwanga, 2003].

The central transect was established to census monkeys not far from Ngogo camp, not for systematic sampling of the chimpanzees' home range, the extent of which was unknown. Teelen [2007b] set up three other transects to increase coverage of the middle of this home range and to sample peripheral areas. The mean number of groups observed per kilometer varied significantly among transects: means were lowest for the central transect and a near-western one also near the home range center, and three to four times higher for transects in peripheral areas to the north and southeast. This raised the possibility that the population decline was specific to the center of the study area.

Here, we re-assess population trends for red colobus, mangabeys, and redbtails in the Ngogo study area using a more "chimpanzee-centric" metric, the

rate at which observers encountered monkey groups while following chimpanzees. The data cover only 1998–2012 and thus have less historical depth than Lwanga et al. [2011], and we do not have updated data from Teelen's three added transects and cannot directly assess population changes in those areas. Nevertheless, they cover the entire chimpanzee home range and thus provide an important check on, and complement to, those of Lwanga et al. [2011].

METHODS

Study Site and Study Populations

Kibale National Park is in southwestern Uganda between 0°13'–0° 41' N and 30°19'–30° 32' E. The 795 km² park is mostly covered by moist evergreen or semi-deciduous forest transitional between lowland and montane forest [Struhsaker, 1997]. The Ngogo study area, in central Kibale, is mostly a mosaic of dry-ground forest at various successional stages, including large tracts of old growth forest adjacent to areas of early- to mid-stage colonizing forest that were grasslands until 1955 or later [Lwanga, 2003]. It also includes swamp forest, bush dominated by *Acanthus pubescens*, papyrus [*Cyperus papyrus*] swamp, and anthropogenic grasslands [Lwanga et al., 2000]. Chimpanzees use all vegetation types [Lwanga, 2003], but mostly use old-growth forest.

Six diurnal primate species besides chimpanzees and red colobus occur at Ngogo [Struhsaker, 1975]: black and white colobus (*Colobus guereza*), redtail monkeys (*Cercopithecus ascanius*), blue monkeys (*Cercopithecus mitis stuhlmanii*), L'Hoest's monkeys (*Cercopithecus lhoesti*), grey-cheeked mangabeys (*L. albigena*), and baboons (*Papio anubis*). Chimpanzees prey on all, but red colobus account for most hunts and the vast majority of prey captures [Mitani & Watts, 1999, 2001, 2005; Watts & Mitani, 2002a,b; unpubl. Ngogo data]. T. Struhsaker systematically censused these eight species along the "central" transect during 23 months in 1975–1976. Subsequent researchers used the same methods to sample group densities along this transect, thereby generating the 380 censuses analyzed by Lwanga et al. [2011].

The Ngogo chimpanzee community has been observed continuously since mid-1995. It is the largest ever documented and has had between about 142 and 189 members, including 22–32 adult males and about 42–52 adult females, during this time [Langergraber et al., 2009; D. Watts, pers. observ.]. Ghiglieri [1984] did the first chimpanzee research at Ngogo in 1978–1979, but could not reliably follow the chimpanzees and saw no hunts. Research and habituation efforts resumed in 1991 and data on hunting started to accumulate in 1995, when all adult males and some adolescent males became well habituated [Mitani & Watts, 1999]. Almost all

community members are now also well habituated, and all tolerate observers when they are with other chimpanzees. All data presented here come from direct observations.

Data on Encounters Between Chimpanzees and Monkeys

Between October 7, 1998, and August 19, 2012, D. Watts noted all visual encounters between chimpanzees and monkeys during 1,348 days of fieldwork. He also recorded the number and identities of all adult and adolescent chimpanzees present and whether the chimpanzees hunted. He also noted all "hunting patrols", which are common at Ngogo [Watts & Mitani, 2002a], regardless of whether patrolling chimpanzees encountered red colobus. Field seasons varied from 2.5 to 10.5 months, and total observation time was 13,536 hr in 58 months. For each monkey species, we first calculated encounter rates as simple ratios of the number of encounters per day to the number of observation hours per day. We used these data to calculate mean daily encounter rates for each month and for the entire study period for red colobus, mangabeys, and redbills. The chimpanzees often encounter mangabeys and redbills, but few encounters lead to hunts [Watts & Mitani, 2002a, unpubl. data]. For this reason and because neither Teelen [2007a] nor Lwanga et al. [2011] could find plausible ecological reasons other than chimpanzee predation for apparent changes in red colobus density, they make good comparative cases for analysis of changes in red colobus encounter rates. We do not include data on encounter rates for other species. Chimpanzees hunt black and white colobus at relatively high rates per encounter [Watts & Mitani, 2002a], but guereza population density is low at Ngogo [Lwanga et al., 2011] and encounters and hunts are uncommon. Group densities of *C. mitis* and *C. lhoesti* are also quite low [*ibid.*], and the chimpanzees often encounter baboons, but rarely hunt them [Watts & Mitani, 2002a]. Below, "days since start" refers to the consecutive ordinal values of observation days starting from October 7, 1998, and "months since start" refers to the consecutive ordinal values of observation months starting with October 1998.

Encounter rate estimates are conservative and not strictly comparable to those from censuses. The chimpanzees must sometimes see monkeys when human observers do not. As during censuses [Lwanga et al., 2011], we excluded encounters that were only auditory; the chimpanzees can use these to locate prey, but DW could not always determine which species produced auditory cues and chimpanzees undoubtedly sometimes hear such cues when humans do not. In contrast to census methods, DW used the chimpanzees' pace, not a slow, steady one, and did not measure distance traveled per unit time or

sighting distances. This could have reduced the probability of seeing monkeys when the chimpanzees were moving quickly, and it means that we cannot provide data on group densities, unlike Lwanga et al. [2011]. Finally, red colobus sometimes seem to hide from approaching chimpanzees by falling silent and climbing high in the canopy [Teelen, 2005], which makes it less likely that observers see them, and other species sometimes flee approaching chimpanzees (indeed, monkey sightings were conspicuously absent on some days when observers followed large, noisy chimpanzee parties long distances). But any biases should not have applied unequally to red colobus or have become more or less pronounced over time. The data provide the best possible chimpanzee-centered estimate of encounter rates and estimate group density from the chimpanzees' perspective because they are based on average travel rates and reflect average search time per encounter.

Encounter Locations

We recorded encounter locations systematically for red colobus only. We recorded GPS coordinates for most, but sometimes just noted the nearest intersection in the trail network and used its previously mapped coordinates to approximate the location. We used two home range measures derived from other GPS-based data sets on chimpanzee habitat use at Ngogo [Amsler, 2009, 2010; Mitani et al., 2010] to look for temporal trends in encounter locations: (1) the 80% minimum convex polygon (MCP) core area of the chimpanzee home range during 2003–2006, mid-way through the interval covered here (“core area”, below), and (2) the 100% MCP home range area during the longer interval from 1999 to 2008 (“HR” below). We used the Home Range Extension to ArcView 3.3 [Hooge & Eichenlaub, 1997] to estimate the 80% core area and 100% HR. We used Hawth's Analysis Tools for ArcGIS 9.1 [Beyer, 2004] to calculate the distances of each red colobus encounter data point from the centroids of both the core area and the HR. We also classified each encounter location as inside or outside the 2003–2006 core area.

Statistical Analysis

As is often true for census data [Lwanga et al., 2011], encounter rates were Poisson-distributed (most daily values for red colobus were zero). Following Lwanga et al. [*ibid.*], we added 0.01 to daily values and to calculate standardized encounter rates (encounters per hour), then used the square roots of standardized values in statistical analyses. Transformed standardized values for red colobus were significantly heteroskedastic (Breusch–Pagan test: $\chi^2 = 26.98$, $df = 1$, $p < 0.001$), with encounter rates becoming less variable over time ($t = -9.27$, $p < 0.001$). Thus, we used robust least squares

regression to examine how rates changed over time, with the transformed standardized daily encounter rate as the response variable and days since the start of the study as the predictor. Redtail encounter rates were also significantly heteroskedastic (Breusch–Pagan test: $\chi^2 = 16.33$, $df = 1$, $p < 0.001$), so we also used robust linear regression to examine the relationship between these rates and days since the study's start. Transformed standardized mangabey encounter rates were not significantly heteroskedastic (Breusch–Pagan test: $\chi^2 = 0.16$, $df = 1$, $p = 0.692$), so we used ordinary least squares regression to examine their relationship to days since the start of the study.

Regression of monthly means for encounter rates against months since the start of the study gave results similar to those of analyses using individual days as data points (below), and we use monthly data for graphical illustrations.

Variance in the distance of encounters from the core area centroid was homoscedastic (Breusch–Pagan test: $\chi^2 = 0.61$, $df = 1$, $p = 0.435$), as was variance in the distance of encounters from the HR centroid ($\chi^2 = 1.14$, $df = 1$, $p = 0.287$). To examine whether red colobus encounters became progressively less common near the center of the area within which the chimpanzees spent most of their time and, conversely, more common increasingly far from the center, we used ordinary least squares regressions with either distance from the core area centroid or distance from the HR centroid as the response variable and days since the start as the predictor variable.

We analyzed the location of hunts similarly. Variance in the distance of hunts from the core area centroid was significantly heteroskedastic (Breusch–Pagan test: $\chi^2 = 6.40$, $df = 1$, $p = 0.011$), as was variance in the distance of hunts from the HR centroid (Breusch–Pagan test: $\chi^2 = 7.55$, $df = 1$, $p = 0.006$), so we used robust linear regression to analyze the relationships between how far hunts were from these centroids and days since the start of the study.

We also calculated monthly hunting rates (hunts per observation hour per month) and prey capture rates (kills per hour per month). To examine temporal trends in these rates, we used them as response variables in ordinary least squares regressions in which months since the start of the study was the predictor. We could not directly count all prey captures for the entire 1998–2012 period because observations were intermittent. The monthly kill rate was significantly related to months since start of the study (below), and we used the regression equation to generate predicted kill rates for all months, including those for which we lacked observations, and then to estimate the number of prey killed per month, assuming a 10 hr daily activity period (the chimpanzees are typically active longer, but the earliest observed red colobus hunt occurred at 08:30 hr and the latest at 18:30 hr). We used ordinary least squares regression to examine the

relationship between resulting estimated cumulative prey offtake values and monthly red colobus encounter rates.

We used STATA v10 [StataCorp, 2007] for statistical analyses. Although Lwanga et al. [2011] reported significant changes in group densities of all three species included in our analysis, we set alpha at 0.05 rather than predict that their results held for the entire study area.

This research was approved by the Yale University IACUC Committee (PHS assurance number A3230-01) and by the Uganda Wildlife Authority, the Ugandan National Council on Science and Technology, and Makerere University. This research complied with the legal requirements of Uganda and adhered to the principles of the American Society of Primatologists for the ethical treatment of primates.

RESULTS

Encounter Frequencies and Temporal Variation in Encounter Rates

Chimpanzees encountered red colobus on 269 days (20.0% of all days). This included 112 days with two encounters, nine with three, and two with four, for a total of 416 encounters (Fig. 1). They encountered mangabeys $787\times$ and redtails $1,570\times$. Mean daily encounter rates were 0.031/hr for red colobus (SD = 0.059, range 0–0.502), 0.059/hr for mangabeys (SD = 0.076, range = 0–0.966), and 0.116/hr for redtails (SD = 0.106, range = 0–0.802). This corresponds to encounters with red colobus once per 32.43 hr, with mangabeys once per 17.20 hr, and with redtails once per 8.62 hr.

The annual red colobus encounter rate declined considerably over time, but not continuously: it peaked in 2002, and then dropped steeply (Fig. 2). It was low during most subsequent field seasons, but rose to a lower peak in 2009. Annual mangabey and redtail encounter rates also varied, but with no clear directional trends (Fig. 2).

The daily rate of red colobus encounters declined significantly as a function of time since the start of the study (robust linear regression: $F_{1, 1338} = 23.93$, $p < 0.001$; Table I). The mean monthly rate of red colobus encounters also decreased significantly with months since the start of the study ($t = -2.47$, $F_{1, 56} = 6.08$, $p = 0.017$; Fig. 3), although this relationship accounted for little of the variance ($r^2_{\text{adj}} = 0.082$). The mean daily rate of redtail encounters did not change significantly over time (robust linear regression: $F_{1, 1338} = 3.33$, $p = 0.068$; Table I), nor did the mean monthly encounter rate ($F_{1, 56} = 0.38$, $p = 0.543$; Fig. 3). Likewise, daily and monthly mangabey encounter rates were independent of the number of months since the study's start (ordinary least squares regressions: $F_{1, 1338} = 0.78$,

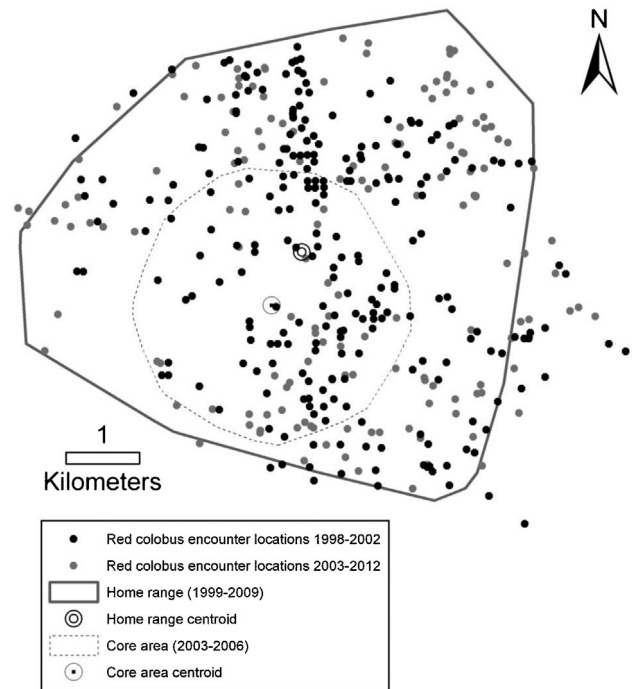


Fig. 1. Locations of chimpanzee-red colobus encounters. Solid black line shows the Ngogo chimpanzee home range from 1999 until 2009, defined using the minimum convex polygon method [Amsler, 2010] and excluding the area of home range expansion identified in 2009 [Mitani et al., 2010]. Centroids for the home range and for the 2003–2006 core area as described in text. Encounters that occurred before or during the 2002 peak in predation and those after 2002 are shown separately.

$p = 0.379$ for daily rate (Table I); $F_{1, 56} = 1.12$, $p = 0.294$; for monthly rate (Fig. 3).

Location of Red Colobus Encounters

More red colobus encounters occurred outside the core area ($n = 273$) than within it ($n = 143$). Over time, encounters took place increasingly far from the core area centroid (robust linear regression: $F_{1, 416} = 53.25$, $p < 0.0001$; Table I, Fig. 4). Encounters also occurred increasingly far from the HR centroid as time passed (robust linear regression: $F_{1, 416} = 58.37$, $p < 0.0001$; Table I, Fig. 4).

The proportions of encounters within versus outside of the core area varied significantly among three periods centered on 2002, when hunting rates and predation pressure were highest (1998–2001; 2002; 2003–2012; $\chi^2 = 20.91$, $df = 2$, $p < 0.001$; Fig. 5). Even in 1998–2001, many encounters were in peripheral areas, partly because many occurred during hunting patrols, but most were in peripheral areas from 2002 on (Fig. 5).

Temporal Variation in Hunting Rates, Prey Offtake, and Hunt Locations

The chimpanzees hunted red colobus on 182 of 416 encounters. They caught at least one red colobus

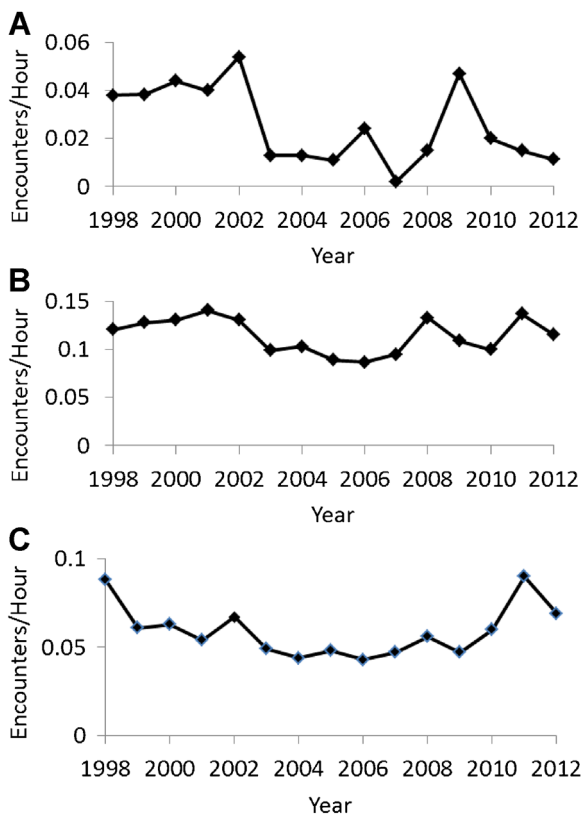


Fig. 2. Mean annual encounter rates between chimpanzees and (A) red colobus; (B) redtails; and (C) grey-cheeked mangabeys.

in 158 of the 182 hunts and captured 616 prey. The hunting rate (hunts per hour per month) decreased significantly over time (ordinary least squares regression: $F_{1, 56} = 6.59, p = 0.013$; Table II, Fig. 6). Correspondingly, the monthly prey offtake rate (number of red colobus killed per hour per month) also declined (ordinary least squares regression: $F_{1, 56} = 10.08, p = 0.002$; Table II, Fig. 6). Using the regression equation to estimate the number of kills per month for months without data on hunting yields an estimate of 2,475 red colobus killed during the entire study. The monthly red colobus encounter

rate decreased significantly as the estimated cumulative total number of kills increased (ordinary least squares regression: $t = -2.54, F_{1, 56} = 6.43, p = 0.014, r^2_{adj} = 0.087$).

The distance of hunt locations from the core area centroid increased significantly over time (robust linear regression: $F_{1, 181} = 26.82, p < 0.0001$; Table I; Fig. 7). The distance of hunts from the HR centroid also increased significantly (robust linear regression: $F_{1, 181} = 22.41, p < 0.001$; Table I, Fig. 7). More hunts occurred outside the core area (132) than within it (51) overall and in each of the three major sub-periods (1999–2001, 2002, 2003–2012), and the proportions of hunts that were inside versus outside the core area did not vary significantly among these three periods ($\chi^2 = 3.41, df = 2, p = 0.183$; Fig. 5).

Hunting Patrols

Of 418 red colobus encounters, 171 (40.9%) occurred during hunting patrols. Patrols led to 48/100 encounters (48.0%) during 2002, when hunting and kill rates peaked. This was not significantly different from the proportion of encounters during patrols in 1998–2001 (58/157, 36.9%) or 2003–2012 (65/161, 40.4%), nor did proportions differ significantly between the 1998–2001 and 2003–2012 periods ($\chi^2 = 3.12, df = 2, p = 0.210$). Monthly patrol rates (mean = 0.011/h, SD = 0.008; median = 0.009) did not vary significantly over time (ordinary least squares regression: $F_{1, 56} = 0.43, p = 0.513$; Table II). The maximum rate of 0.034 patrols/hr (one patrol per 30 hr) coincided with the maximum hunting rate of 0.065 hunts/hr in June, 2002.

DISCUSSION

Temporal variation in the rate of encounters between chimpanzees and red colobus monkeys at Ngogo corroborates census data collected by Teelen [2007b] and Lwanga et al. [2011] and strengthens their conclusion that the local red colobus population has declined significantly since 1998 and probably since 1975 [*ibid.*]. Both Teelen [2007b, 2008] and

TABLE I. Results of Regressions of Encounter Rates and of the Distances of Red Colobus Encounters and Hunts From the Home Range (HR) and Core Area (CA) Centroids on Days Since the Start of the Study

Response variable	Coefficient (SE)	t value	p
Red colobus encounter rate	-0.000012 (2.42 ⁻⁶)	-4.89	<0.0001
Redtail encounter rate	-0.000040 (3.39 ⁻⁶)	-1.82	0.068
Mangabey encounter rate	-0.000003 (2.95 ⁻⁶)	-0.88	0.379
Distance of red colobus encounters from HR centroid	.2296 (0.0301)	7.64	<0.0001
Distance of red colobus encounters from CA centroid	0.2223 (0.0334)	7.30	<0.0001
Distance of hunts from HR centroid	0.2262	4.67	<0.0001
Distance of hunts from CA centroid	0.2480 (0.0479)	5.18	<0.0001

All but mangabey encounter rates based on robust least squares regressions, for which R^2 values are not given.

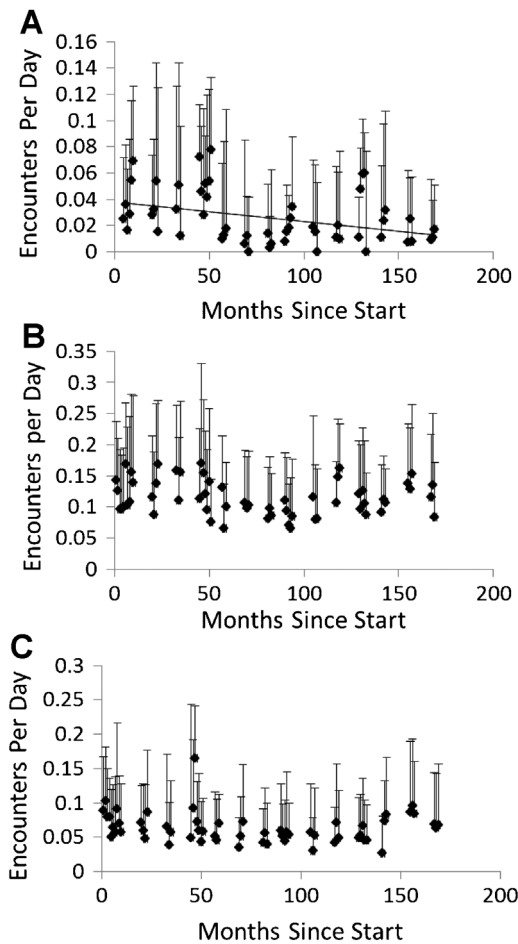


Fig. 3. Mean monthly encounter rates between chimpanzees and (A) red colobus; (B) redtails; and (C) grey-cheeked mangabeys. Vertical bars show 1 SD.

Lwanga et al. [2011] argued that changes in food abundance were unlikely to explain the population decline and that the most likely explanation was predation by chimpanzees. Our data are consistent. Predation by chimpanzees has undoubtedly accounted for a substantial proportion of red colobus mortality [Teelen, 2008; Watts & Mitani, 2002a,b], although hunting rates and rates at which the chimpanzees killed red colobus have decreased as they have encountered red colobus at increasingly lower rates.

In contrast to Lwanga et al. [2011], we found no evidence of group density increases for redtails and mangabeys. The central census route encloses a large area of former grassland, and censuses there have presumably captured a long-term grassland replacement effect on redtail demography. However, most of the study area is covered by older forest and this effect might not be widespread. Reasons for the discrepancy in mangabey encounters are less obvious, but it could be associated with high abundance of

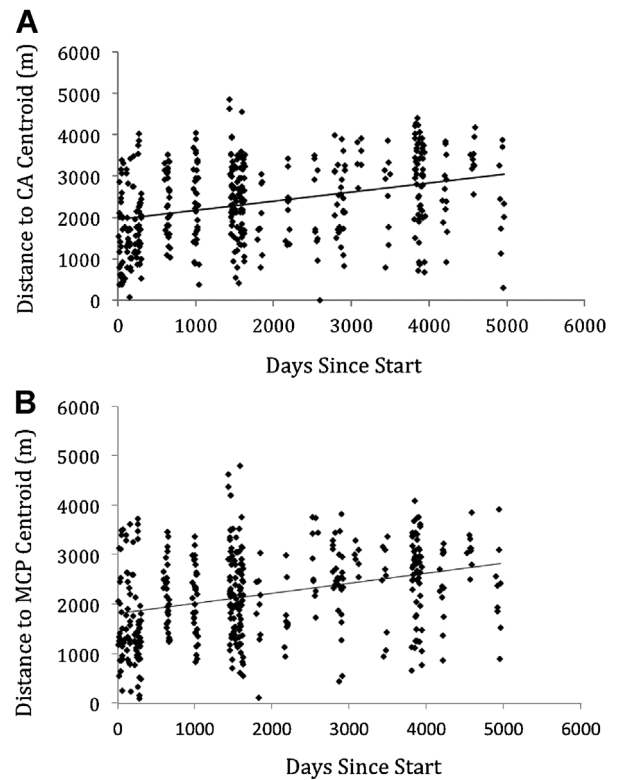


Fig. 4. Distance of red colobus encounters from (A) the centroid of the 80% core area of the chimpanzee home range in 2005–2006 and (B) the centroid of the 100% minimum convex polygon home range between 1998 and 2009.

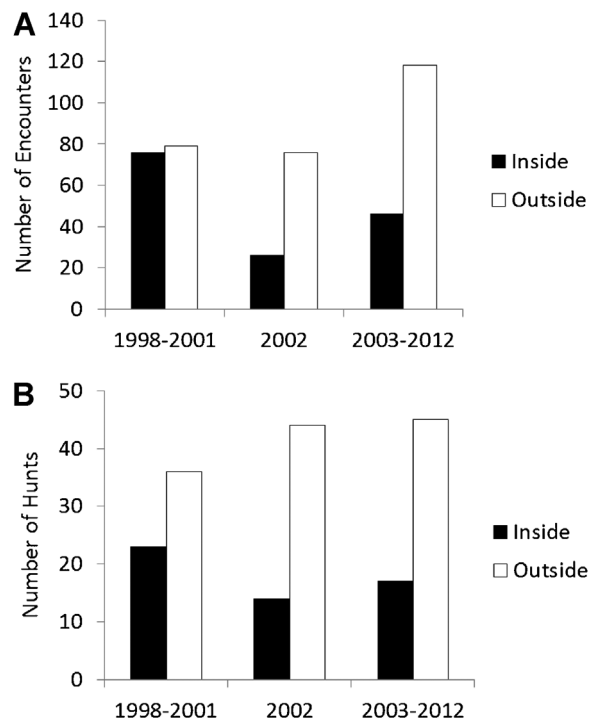


Fig. 5. The frequency of (A) encounters with red colobus groups and (B) red colobus hunts that were inside (black bars) or outside (open bars) the 80% core area.

TABLE II. Results of Ordinary Least Squares Regressions of Red Colobus Hunting and Offtake Rates and of Hunting Patrol Rates on Months Since the Start of the Study

Response variable	Coefficient (SE)	<i>t</i> value	<i>p</i>	R^2_{adj}
Hunts/h/month	-0.00008 (0.00003)	-2.57	0.013	0.089
Kills/h/month	-0.00034 (0.00011)	-3.17	0.002	0.137
Patrols/h/month	-0.000014 (0.000013)	-0.66	0.513	0.010

important food species (notably *Uvariopsis congensis*) along the central transect.

Even though encounter rate data are not equivalent to census data, several results imply that they truly reflect a red colobus population decline. First, the average distances of encounter and hunt locations from chimpanzee activity centroids increased over time, as expected if prey availability was depleted in relatively heavily used areas, including those covered by the central census route and by Teelen’s [2007b] near-western transect. Also, both hunting and prey offtake rates decreased, even though the number of chimpanzees (in particular, the number of adult males) increased. Finally, data on encounter rates during hunting patrols suggest that the red colobus population has been depleted even in peripheral areas. The chimpanzees travel substantial distances during patrols, usually in peripheral areas, and often enter overlap areas and

sometimes make incursions into neighboring territories. If red colobus group densities remained stable or increased in these areas while they decreased closer to the home range center, the proportion of encounters that occurred during patrols should have increased as encounters became less common overall. However, it remained stable. This cannot be explained by a decrease in patrolling, because the rate of patrolling did not vary significantly. Still, we need long-term census data to assess red colobus density trends in peripheral areas accurately.

Encounter rates are the best measure of actual hunting opportunities. But while time since the study’s start was significantly related to encounter and hunting rates, distances to encounters and hunts, and prey offtake rates, it explained little of the variation in these factors. Variation in travel rate and directionality and in chimpanzee party size presumably also influences encounter rates. Monkey

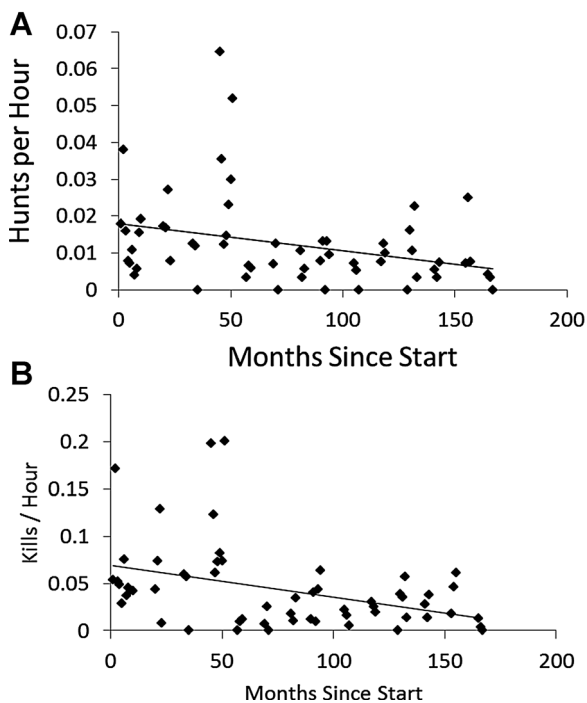


Fig. 6. Monthly red colobus hunting rates (hunts per hour per month) and prey offtake rates (kills per hour per month) during the study.

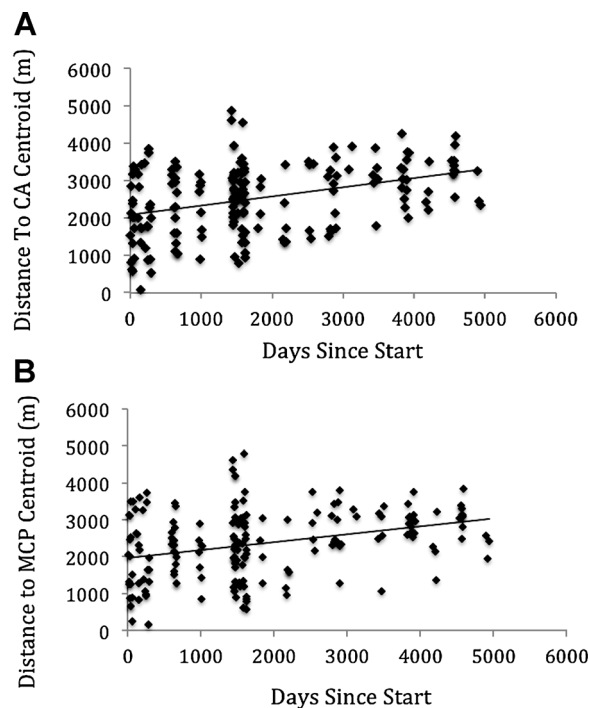


Fig. 7. Distance of red colobus hunts from (A) the centroid of the 80% core area of the chimpanzee home range in 2005–2006 (“CA Centroid”) and (B) the centroid of the 100% minimum convex polygon home range (“MCP Centroid”) between 1998 and 2009.

groups may become less conspicuous when they detect large, noisy chimpanzee parties. In turn, party size depends partly on the availability of fruit and of estrous females [Mitani et al., 2002]. Also, chimpanzees are presumably less likely to encounter a red colobus group on a day when they travel only 1 km than on a day when they travel 4 km.

The steep decline in red colobus encounter rates between 2002 and 2003 and the increase during 2009 deserve comment. Predation intensity peaked in 2002 [Teelen, 2008] and probably led to several group extinctions; even a single extinction near the central census route could have accounted for the post-2002 asymptote documented by Lwanga et al. [2011]. Chimpanzee researchers encountered several groups in this area in the mid-to-late 1990s, but only one has used it recently. The 2009 increase coincided with a major expansion of the chimpanzee territory to the east and northeast after years of intense boundary patrolling and many fatal attacks on members of one or more neighboring communities in these areas [Mitani et al., 2010]. Evidence from Ngogo [ibid.], Gombe [Williams et al., 2004], and Kanyawara [Wilson et al., 2012] strongly implicate competition over plant food resources as the main instigator of intergroup encounters in chimpanzees and maintaining or increasing access to food as the main function of lethal coalitionary intergroup aggression. Increased access to vertebrate prey—notably red colobus—may be a side benefit (if perhaps a short-term one) of territory expansion predicated on success in intergroup aggression. Most 2009 encounters occurred in the expansion area. Many were with two groups often present near several clumps of fruiting *Morus mesozygia* trees in which the chimpanzees fed heavily in June, July, and October. The chimpanzees did not hunt these groups, but they hunted several others that they encountered while patrolling or foraging north and east of the *Morus* concentrations.

Teelen [2008] estimated that 15 red colobus groups used the 25 km² within which Ngogo chimpanzees spent most of their time in 2001–2003. Variation in estimated mean group size led her to put total population size at 506–664. Using a range of values for group size and prey offtake rates, she estimated that the chimpanzees killed 15% to 53% of the red colobus population annually. This is far higher than estimates from Tai [3.2–7.6%; Boesch & Boesch-Achermann, 2000] and Mahale [1.1–1.3%; Boesch et al., 2002], although mostly within the range of those for Gombe [16–32%: Stanford, 1996; 42%: Wrangham and Bergman-Riss, 1990]. Teelen's [2008] simulations of projected population numbers showed that documented hunting rates were unsustainable and the population had an extremely high probability of local extinction within 12 years unless the chimpanzees stopped hunting. The territory expanded to 35 km² in 2009 (into areas previously used for

hunting patrols), which could increase Teelen's estimates to about 664–810. Still, estimated total offtake between 1998 and 2012 gives averages of 20.4–24.8% of these numbers killed annually. Such high rates led to high extinction probabilities in most of Teelen's simulations, at least without high thresholds at which hunting stopped and especially if more than a few adult males were killed annually. Teelen also noted that chimpanzees are not obligate carnivores and do not depend on red colobus as food, so predator-prey cycles were unlikely and local red colobus extinction was distinctly possible.

Alternatively, declining density of red colobus groups might induce a threshold effect by increasing search costs enough to reduce offtake to a sustainable level [ibid.]. Long-term data are consistent with this alternative: hunting has not stopped, but hunting rates and offtake have declined, with steep drop-offs after the 2002 peaks. Given the importance of learning for developing hunting skills [Boesch & Boesch-Achermann, 2000], predation pressure may also diminish because cohorts of male chimpanzees maturing after these 2002 peaks become less competent hunters than males who matured earlier.

Whether chimpanzee predation is now low enough to allow the red colobus population to recover remains to be seen. The absence of substantial declines in red colobus food availability at Ngogo [Lwanga et al., 2011; Teelen, 2007b] combined with the low population density should make the area attractive to females dispersing from surrounding areas with higher population densities and to groups in such areas that could expand or shift their home ranges. Any resulting source-sink population dynamics might be analogous to those associated with local depletion, but not regional extirpation, of some prey species by Ache subsistence hunters in the Mbarucayu Reserve, Paraguay. Hill et al. [2003] found that prey encounter rates in Mbarucayu increased with increasing distance from heavily-used hunting trails, but concluded that hunting of most taxa seemed sustainable, even though encounter rates declined over time for several (most notably capuchin monkeys). However, we cannot assume the entire surrounding area is a good source of dispersing individuals and expanding groups. Most adjoining chimpanzee communities are unhabituated and their size or composition is uncertain, but the habituated Kanyanchu community has over 100 members and an unhabituated community to the west/southwest is also very large and has many adult males. In recent years, red colobus encounters where its home range overlaps that of the Ngogo community have been strikingly rare and several groups seem to have disappeared. This is consistent with the hypothesis that Ngogo chimpanzees have caused a decline in the red colobus population throughout their home range, but hunting by members of the neighboring community might have exacerbated the decline. Combined

with the relatively high frequency of hunting patrols, such an effect would mean that overlap areas are not refuges for the red colobus, contrary to what Stanford [1995] reported for Gombe. It would also provide another, poignant parallel to the situation facing Ache subsistence hunters, who may harvest prey at rates that should be sustainable, but cannot control the behavior of outsiders who hunt illegally in their reserve and whose activities may make overall harvest levels unsustainable [Hill et al., 2003].

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