American Journal of Primatology 74:602–612 (2012)

RESEARCH ARTICLE

Reductions in Primate Abundance and Diversity in a Multiuse Protected Area: Synergistic Impacts of Hunting and Logging in a Congo Basin Forest

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This article explores spatial and temporal changes in diurnal primate abundance and behavior in response to hunting, logging, and conservation at the Dzanga Sangha Dense Forest Reserve (RDS), Central African Republic over time. We use a combination of line-transect surveys in 2002 and 2009 ($N = 540$ km) and ethnographic interviews ($N = 210$) to investigate changes in the status of cercopithecines and colobines at RDS, with additional comparisons to earlier work. This protected area was lightly logged in the 1970s and the park was gazetted in 1990, with multiple-use reserve sectors allocated. Since the park's inception, hunting and the trade of primates have increased, along with human migration, greater accessibility of arms, and reduction of preferred ungulate prey. Primates have declined in both the park and reserve sectors. Our data further suggest that at RDS hunting has had a greater impact on primate diversity and abundance than logging. We have identified changes in species-specific vulnerability to hunting over time, with *Cercopithecus nictitans* and *Lophocebus albigena* initially having appeared to be relatively resistant to hunting pressure in 2002. However, subsequently as gun hunting has increased at RDS, these species have become vulnerable. Although monkeys at RDS have been responding behaviorally to increased gun hunting, they are not able to keep pace with changing hunting practices. This study allows us to begin to understand synergistic impacts of hunting and logging, necessary if we are to recommend strategies to better secure the future of primates in multiuse protected areas. Am. J. Primatol. 74:602–612, 2012. © 2012 Wiley Periodicals, Inc.

Key words: Central Africa; conservation management; guns; primate communities

INTRODUCTION

Long-term studies on the effects of logging and other habitat disturbances on African monkeys reveal a high degree of variability between sites and species [Chapman et al., 2010; Mammides et al., 2008; Plumptre & Johns, 2001]. While primates are often negatively affected by heavy logging, some species can tolerate or even thrive in lightly logged forests [Chapman et al., 2010] or in regenerating fields [Baya & Storch, 2010; Tutin et al., 1997]. These studies have articulated the effects of logging on primate populations, but they have been conducted in sites where primates are not also subject to human hunting pressure [but see Wilkie et al., 2001].

The most significant effects of logging on forest mammals in the Congo Basin are likely the indirect effects of road development and hunting [Laurance et al., 2006; Wilkie et al., 2000]. Most human populations in the Congo Basin rely on wild game meat for protein needs [Bennett et al., 2007; Bowen-Jones & Pendry, 1999; Eves & Bakaar, 2001]. Levels of wild game consumption vary with local ecology and subsistence practices, economics, and existing cultural preferences [Daspit, 2011; Wilkie et al., 2005]. Greater accessibility of arms, ammunition, and remote forest areas have all increased commercial hunting and wildlife trade in the Congo Basin [Allebone-Webb et al., 2011; Linder & Oates, 2011; Oglethorpe et al., 2007].

Primate harvest rates are influenced by relative abundance, ease of capture, and access to hunting technology [Fa & Brown, 2009; Fa et al., 2005; Kumpel, 2006; Refisch & Kone, 2005]. Primates have low intrinsic rates of population increase, and thus are likely to decline wherever they become targets of gun hunters [Linder & Oates, 2011], and they

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Contract grant sponsor: WennerGren Foundation; Contract grant sponsor: L.S.B. Leakey Foundation; Contract grant sponsor: National Geographic Society; Contract grant sponsor: New York Consortium in Evolutionary Primatology; Contract grant sponsor: Collegiate Research Scholar Grant from the Dean's Undergraduate Research Fund at New York University; Contract grant sponsor: Molecular Primatology Laboratory.

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Received 25 July 2011; revised 9 January 2012; revision accepted 11 January 2012

DOI 10.1002/ajp.22012

are vulnerable to extirpation [Cowlishaw & Dunbar, 2000]. In addition, primates may show behavioral responses to human hunters, becoming more cryptic by reducing calling rates and hiding from observers [Croes et al., 2006; Kumpel et al., 2008]. At Tai Forest, Cote d'Ivoire, monkeys modified their antipredator behaviors and used lower substrates to avoid detection by human hunters [Kone & Refisch, 2007].

This article explores temporal and spatial changes in primate abundance and behavior at the Dzanga-Sangha Dense Forest Reserve (RDS), Central African Republic 2002–2009 with additional comparisons from 1986 to 2009. We use long-term census data to address how logging and hunting differentially impact primate communities in a multiple-use forest. RDS was selectively logged at low intensity in the 1970s and again between 2002 and 2005; however, the potential long-term impacts have not been addressed for monkeys in this region. Human in-migration to RDS [Blom et al., 2004], greater access to arms, and reduction of preferred ungulate prey have led to increased hunting and trade of primates [Daspit, 2011; Fa et al., 2005; Jost Robinson et al., 2011]. The sustainability of hunting practices at RDS will be critical to securing the future of monkey populations, small- and medium-sized ungulates, as well as the more vulnerable apes and elephants [Eves, 2001; Robinson & Bennett 2000]. This article focuses on *Cercopithecus pogonias*, *C. nictitans*, *C. cephus*, *Lophocebus albigena*, and *Cercocebus agilis*.

Monkey communities in the Dzanga Park and adjacent reserve have been subject to long-term hunting pressure and are difficult to study. Our repeated line-transect surveys over a 7-year period and hunter interviews allow us to document temporal and spatial changes in primate abundance and community structure. We also explore behavioral plasticity among monkeys in response to varied human disturbances, particularly an increase in gun hunting. We must tease apart impacts of hunting and logging [Wilkie et al., 2001] if we are to understand the likelihood of a possible future for Central African forests without primates or to formulate management plans that include certified logging practices or the possibility for more sustainable hunting [Chapman & Onderdonk, 1998; Elkan et al., 2006].

METHODS

Study Site

Conservation and development activities in the southwestern Central African Republic began in the mid-1980s [Carroll, 1986] with the Dzanga-Sangha Dense Forest Reserve (RDS) officially designated as a park (1,200 km^2) and multiple-use reserve (3,360 km^2) in 1990 (Fig. 1). Only research and tourism are officially permitted within the RDS park (Dzanga and Ndoki). Cable snares are prohibited throughout RDS. In the reserve, gathering of plant and animal products, traditional spear, crossbow and net hunts, as well as regulated shotgun hunting during daylight hours are permitted.

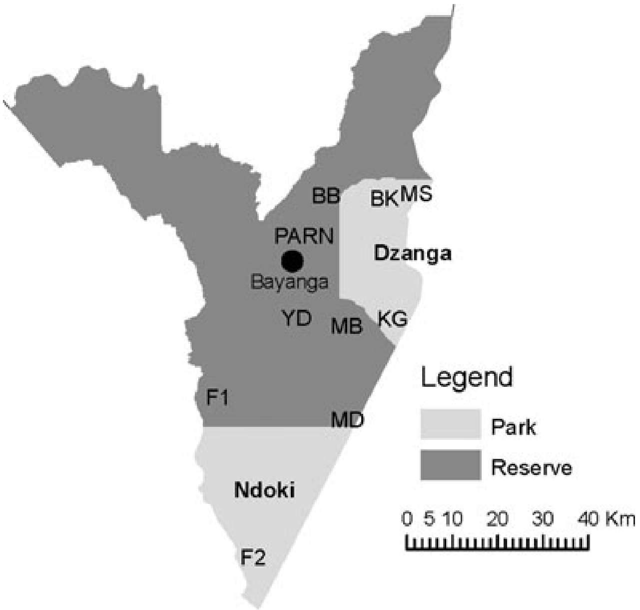

Fig. 1. Map of Dzanga-Sangha Dense Forest Reserve (RDS), Central African Republic (CAR). Data courtesy of APDS. Field sites included in 2002 versus 2009 comparison: Kongana (KG), Mabongo (MB), Mossapoula Source (MS). Field sites included in larger comparisons: Bakombo (BK), Babongo (BB), Yandoumbe (YD), PARN, F1 and F2 (census sites for Fay (1986)), and Mondika (MD). The village of Bayanga is the central human population center in RDS.

Much of the RDS including current park and reserve sectors was selectively logged (mainly *Entandrophragma* sp.) at low intensity from 1975 to 1982. Only reserve sectors were logged again from 2002 to 2004. Human populations have been estimated at 5,000, but have fluctuated dramatically with logging-related employment opportunities in the region [Kamis, 2006; Noss, 1998]. Although wire snares were the predominant mode of hunting through the 1990s at RDS [Noss, 1998; Remis, 2000], guns have now largely replaced wire snares, spears, and nets. Gun hunting at RDS has increased at least fivefold since 2006 [Jost Robinson, unpublished]. Guns make primates more accessible prey; in 2008, primates represented 23% of the meat for sale at the local RDS market, relative to 9% in 2006 [Jost Robinson et al., 2011].

Rainfall at RDS averages 1,400 mm/ year. The forests can be broadly classified as mixed secondary forest (low-canopy forest with dense understory), although mixed primary forest (high-canopy forest with a relatively open understory) is also common. We also recorded monodominant stands of *Gilbertiodendron dewevrei* (locally known as malapa) forest, logging or elephant-created gaps, streamside forests, and marshy clearings as habitat types every 50 m along transects [Remis, 2000].

All research contained in this manuscript complied with protocols approved by the Purdue Animal Care and Use Committee and adhered to the legal requirements of the Central African Republic. The research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Nonhuman Primates.

Field Data Collection

Line-transect surveys

Using line-transect surveys [Plumptre, 2000; Plumptre & Cox, 2006], we monitored large mammal species including diurnal primates (*C. pogonias*, *C. nictitans*, *C. cephus*, *C. neglectus*, *L. albigena*, *C. agilis*, *Colobus guereza*, *Procolobus badius*, *Pan troglodytes*, and *Gorilla gorilla*) at intervals from July–August 1997 (Park = 42 km; Reserve = 39 km); January–April 2002 (Park = 240 km; Reserve = 165 km); and August 2008–June 2009 (Park = 77.2 km, Reserve = 58.2 km) (see Table I). Here, we initially compare primate abundance and hunting sign encounter rates from two RDS parks (MS: Mossapoula Source; KG: Kongana) and one reserve (MB: Mabongo) sites that were established at varying distances from the main human population center in Bayanga and surveyed by each of us (Remis in 1997 and 2002; Jost Robinson in 2008–2009) using the same methods.

At each of our research sites, we established four to six 5-km line transects, perpendicular to drainage patterns, using an abandoned primary logging road as a baseline (in 2009, RDS the number of transects that could be reopened within the park were limited). At each site, we located at least two transects within 500 m of and parallel to a secondary logging road, and two more than a kilometer from the nearest secondary road. Following methods described in White and Edwards [2000], teams of at least two observers walked transects between 0700 and 1300 hr at a pace of 1 km/hr. Remis originally trained transect teams in 1997 and again in 2002; Jost Robinson retrained them and added additional workers in 2008–2009. One of our primary research assistants, Jean Bosco Kpanou (J.B.K.) was present during the original RDS censuses by Carroll and Fay in the 1980s. He and Bruno Bokoto DeSemboli (B.B.D.) subsequently received additional training during their participation in regional census work. Remis or Jost Robinson was present on all 1997, 2002, and 2008–2009 transects. On the transects, we documented direct observations of nonhuman primates noting species, age/sex (if possible), location on transect, perpendicular distance from transect, and animal–observer distance [Fashing & Cords, 2000; Marshall et al., 2008]. During data collection, we also recorded all indications of human activity on transects, including logging and hunting signs (indication of logging trails, stump cuts, snare or gun use) and other human traces.

Hunter off-take and interview data

Ethnographic semistructured interviews (N = 210) with hunters from Bayanga and nearby villages within RDS included information on hunting methods, preference, and returns, as well as their knowledge of the behavioral and population responses of hunted wildlife species. Given the potentially sensitive nature of hunting-related topics, we used snowball sampling to opportunistically select individuals who were willing to participate in this study [Bernard, 2002; Trotter & Schensul, 1998]. In snowball sampling, the researcher employs a group of primary informants to facilitate connections with additional members of the community. This method of subject recruitment is the most appropriate for establishing a relationship with hunters when there is the potential for an informant to divulge sensitive information because some forms of hunting are illegal in protected areas. Snowball sampling was chosen to minimize the risk to human participants in accordance with protocols from the Institutional Review Board on use of human subjects. Thirty-four weeks of surveys with 15 local hunters (cable = 5, registered firearm = 5, artisanal firearm = 5) yielded data for 793 hunting trips. Surveys included data on munitions taken, animals captured by age (adult/juvenile) and sex class.

Data Analysis

For the analyses that follow, we employed encounter rates of observations of monkey groups per kilometer of transect. In many cases, small sample sizes and low encounter rates prevented us from conducting species-specific density analyses [Buckland et al., 2010]. Encounter rates facilitated comparisons on our study transects over time and allowed us to compare our results to those of other studies conducted within RDS, as has been done for long-term research at Kibale National Park, Uganda [Lwanga et al., 2011]. We acknowledge that the use of encounter rates has been criticized because of the possibility of interobserver differences and differential visibility on transects that can influence detection and strip width [Remis & Hardin, 2009]. However, we maintained at least two trained observers on teams between field seasons and did not find any statistically significant differences in estimated strip width between transects. Nevertheless, encounter rates should be interpreted with caution, as they may also be influenced by potential differences in detectability of primates under varying conditions of human disturbance.

TABLE I. Average Encounter Rates (Observations of Groups/km) of Monkey Groups on Transects[*], 1994–2009

	1994 data Noss (1995) 93 km (six transects; 7–18 repeats)	1999 data Shah (2003) 195 km (one transect; 39 repeats)	2002 405 km (20 transects; four repeats)	2009 135.4 km (20 transects; two repeats)
All species	0.998	0.887	0.769	0.300
Park	—	0.887	1.125	0.340
Reserve	0.998	—	0.531	0.181
C. pogonias	0.052	0.087	0.114	0.033
Park	—	0.087	0.152	0.044
Reserve	0.052	—	0.088	0
C. cephus	0.194	0.154	0.125	0.008
Park	—	0.154	0.156	0
Reserve	0.194	—	0.105	0.030
C. nictitans	0.627	0.308	0.301	0.148
Park	—	0.308	0.403	0.167
Reserve	0.627	—	0.233	0.090
C. neglectus	0	0	0.010	0
Park	—	0	0	0
Reserve	0	—	0.017	0
L. albigena	0.022	0.277	0.100	0.087
Park	—	0.277	0.150	0.086
Reserve	0.022	0	0.066	0.090
C. agilis	0.154	0	0.018	0
Park	—	0	0.007	0
Reserve	0.154	–	0.025	0
C. guereza	0	0	0	0
Park	—	0	0	0
Reserve	0	—	0	0
P. badius	0	0	0	0
Park	—	0	0	0
Reserve	0	—	0	0

[*] In 2009, Jost Robinson added two additional transects to the original four transects put in by Remis at two sites (MY and KG). The addition of transects at sites in 2009 was related to the logistical difficulty of accessing some of the sites previously used by Remis.

We used *G* tests of goodness of fit [Sokal & Rohlf, 1995] to evaluate differences between primate abundance in different sectors from 2002 to 2009 and the relationships between primate abundance and habitat factors. Additional nonparametric statistical tests including Mann–Whitney, Kruskal–Wallis, and Spearman's correlations were performed using SPSS® (18.0.02). All statistical tests were two-tailed.

Following Linder & Oates [2011] we also calculated a hunting response index to assess species-specific differences in vulnerability to hunting pressure. The hunting response index is the ratio of the relative frequency of observations of primates along transects in the most heavily hunted site to their abundance in the least heavily hunted site in each study period.

Longer term comparative data analysis

To extend the time period for temporal and spatial analysis of abundance of monkeys at RDS, we compared our results to studies that used similar methods in previous years at RDS [Noss, 1995; Shah 2003] (Table I). Noss [1995] completed 93 km of repeat walks along six line transects at the forest edge (reserve) within 5 km of Bayanga in 1993/1994 where human hunters were common (Natural Resource Management Project (PARN), Fig. 1). Shah [2003] reported on 195 km of repeated surveys of a 5-km transect in 1999 and 2001 at the remote, unlogged Mondika site (MD: Mondika) in the Ndoki (park sector) on the Congo border, where humans are scarce (Fig. 1). Rainfall, habitat availability, and vegetation are relatively similar throughout RDS, though Mondika has been qualitatively characterized as denser, with lower visibility on the ground than the Dzanga forests [Shah, 2003]. To maximize the usefulness of these comparisons, we included additional transect sites from our larger work to increase comparability between our data sets and those of Shah (2003) and Noss (1995). Specifically, we added two additional reserve transect sites that were close to Bayanga with high human impact (BB: Babongo; YD: Yandoumbe), and another site in the Dzanga Park sector (BK: Bakombo) with low human activity (Fig. 1).

To assess changes in primate community composition at RDS over time 1986–2009, we compared

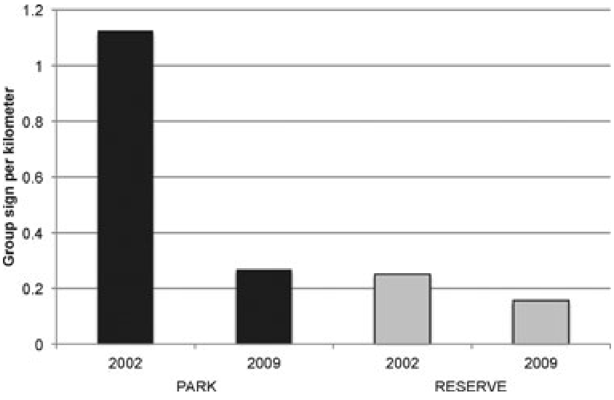

Fig. 2. Primate group observation encounter rates (all species combined) in park and reserve, 2002 versus 2009. Park is depicted in black and reserve in gray. This comparison uses the three RDS transect sites where data were collected in both 2002 and 2009.

the relative representation of primate species (proportions of species A/total observations of all primate species) observed along line transects at RDS across multiple study periods (Table III). We did not attempt to compare abundance (encounter rates or observations/km) of studies that used different methods. Fay's 1986 line-transect survey data [Fay, 1989] and those collected by Remis in 1997 were collected using one-off transects (data collected while opening transects with a machete), which likely reduced encounter rates with monkeys. However, we used these data to examine changes in primate community composition since the inception of RDS and in light of subsequent fluctuations in human populations and hunting practices.

RESULTS

Abundance of Primates at RDS 2002 Versus 2009

We initially compared the abundance of primates recorded along matched repeated walk transects surveyed in three sites in both 2002 and 2009 (MB, KG, and MS, Fig. 1). Seven species of monkeys were observed or heard along transects in 2002 (*C. pogonias*, *C. nictitans*, *C. cephus*, *C. neglectus*, *L. albigena*, *C. agilis*, *and C. guereza*) but in 2009 we found no indication of *C. neglectus*, *C. agilis*, *C. guereza*, *or P. badius* on transect walks (Table I). In both 2002 and 2009, *C. nictitans* was the most vocal species and the one most frequently observed on transects. *Lophocebus albigena* loud calls were also commonly heard. These two large-bodied species were also the most commonly sold in the market [Jost Robinson et al., 2011]. The loud antipredator calls and easy detectability of these monkey species make them easy prey for daytime hunters.

Observations of the most common species of monkeys at RDS, *C. pogonias*, *C. nictitans*, *and C. cephus*, during the line-transect surveys have declined significantly since 2002 (Mann–Whitney test 2002 (12 transects) vs. 2009 (27 transects): *C. nictitans* $U = 99.0$, $P = 0.036$, *C. pogonias*, $U = 88.5$, $P \leq 0.001$, *C. cephus* $U = 101.00$, $P \leq 0.012$, two-tailed tests) (Fig. 2).

Park and reserve 2002 versus 2009

Monkeys had been relatively prevalent in RDS within the Dzanga Park during the 2002 study period [Remis, 2000; Remis & Hardin, 2009]. However, by 2009, monkey abundance on transects had significantly decreased in both the park and reserve (monkey group observations by year, Mann–Whitney U test: $U = 71.5$, transects $N = 12, 27$, $P \leq 0.004$). Overall monkey group abundance along transects was higher in park than reserve sectors in 2002 (monkey group observations/km by park sector 2002, $U = 2.5$, $N = 12$ transects, $P \leq 0.02$). Differences in primate abundance between the supposedly integrally protected park and community hunting reserve areas were no longer apparent in 2009 (Fig. 2).

Our data also indicated that monkey calls along transects have declined since 2002 in both park and reserve, suggesting that monkeys had both become more cryptic and/or were declining. In the combined park and reserve sample, we heard an average of 5.55 (±0.790) monkey vocalizations/km on 2002 transects, whereas in 2009 we heard on average of only 2.52 (± 0.426) vocalizations/km (Mann–Whitney U test calls/km 2002 vs. 2009: $U = 62$, ($N = 12$ transects, 27 transects), $P = 0.001$). Encounter rates with calls did not vary in 2002 between park and reserve (calls/km 2002: $U = 8$, $N = 12$, $P = 0.214$), but in 2009 calls were less frequent in the reserve than in the park (calls/km 2009: $U = 23.5$, $N = 27$ transects, $P = 0.003$).

Factors Influencing Primate Abundance at RDS

To better understand some of the factors influencing patterns of primate abundance at RDS, we examined the potential impacts of distance from Bayanga (as a proxy for hunting pressure), proximity of logging roads, habitat availability, and variations in logging sign on transects on primate abundance. Total monkey observations were positively correlated with distance from Bayanga in the 2002 data set (Spearman's correlation: $r_s = 0.695$, $P = 0.012$, $N = 12$ transects). However, in the 2009 data set, there were no significant correlations between monkey observations overall and distance from Bayanga. At the species-specific level in 2002, encounter rates were correlated with distance for *C. nictitans* (Spearman's correlation: $r_s = 0.654$, $P = 0.025$, $N = 12$ transects); however, this relationship was not present in the 2009 data set. No significant correlations were observed between encounter rates and distance from town for *C. cephus*, *C. pogonias*, *C. agilis*, *L. albigena*, or *C. guereza*. In 2002, monkey observations were negatively correlated with logging sign (Spearman's correlation: $r_s = –0.860$, $P = 0.000$, $N = 12$ transects). Monkey observations were neither positively nor negatively correlated with the frequency of visible hunting sign on transects in 2002. However, in the 2009 data set, these relationships had changed; monkey observations were negatively correlated with hunting (Spearman's correlation: $r_s = –0.814$, $P = 0.000$, $N = 16$ transects), but were no longer correlated with logging sign. Monkey calls were negatively correlated with logging sign in 2002 ($r_s = –0.603$, $P = 0.038$, $N = 12$ transects), but this was no longer the case in 2009.

Impacts of logging on habitat use by monkeys at RDS

To further examine monkeys' use of formerly logged areas, we compared primate encounter rates in 2002 on matched transects close to and far from abandoned secondary logging roads. Low sample size of observations precluded us from conducting this analysis with the 2009 data. Monkeys' presence in logged sites and their greater use of those transects within 500 m from abandoned logging roads relative to those at least 1 km away from logging roads in 2002 (Overall monkey group observations close to logging roads $N = 167/283$, far from logging roads $N = 116/283$; G test of goodness of fit: $G = 10.20$, $\text{df} = 1$, $P \leq 0.001$) suggests they were not negatively impacted by logging itself or forest succession at this time. Further examination of their use of habitat types suggests that they were preferentially selecting logged habitats (60% of observations) relative to their availability (56% of 50-m forest blocks along transects) (G test of goodness of fit: $G = 22.13$, $\text{df} = 5$, $P \leq 0.004$). Therefore, recent declines in primate encounters on roads increasingly used by hunters, and in logged areas after 2002, suggest hunting rather than fragmentation might be responsible.

Hunting vulnerability

Our previously relogged reserve study site (MB) was more intensively hunted than sites in the park (KG and MS) in both study periods. Yet in 2002, primates were present even in forests that were bustling with human hunters. We calculated a hunting response index to understand the relative vulnerability of primates to human hunters in these two periods and to reveal any potential species differences in vulnerability over time. Previous to 2002, *C. pogonias* were least vulnerable to hunting pressure by this index, consistent with local taboos against eating the meat of this species [Kumpel, 2006]. *Cercopithecus nictitans* and *L. albigena* were relatively resistant to hunting pressure in 2002, but by 2009 changes in the hunting index for all primates present at RDS suggested that they had all become vulnerable to the increased hunting pressure in the region (Fig. 3).

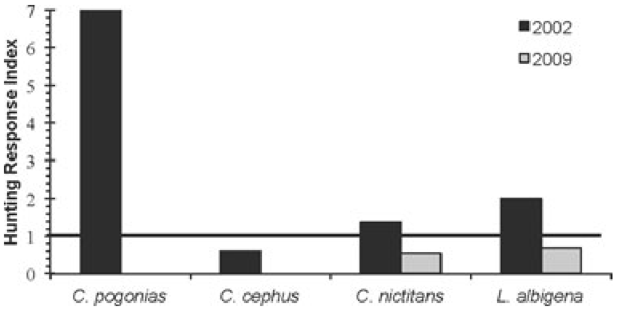

Fig. 3. Changes in hunting vulnerability between monkey species at RDS, 2002–2009. A hunting index score < 1 indicates vulnerability to hunting. Park is depicted in black and reserve in gray. This comparison uses the three RDS transect sites where data were collected in both 2002 and 2009. The hunting index = ratio of the relative frequency of observations of primates along transects in the most heavily hunted site relative to their abundance in the least heavily hunted site. The 2009 data for *Cercopithecus cephus* and *C. pogonias* do not appear given small size.

Hunter Off-take in Relationship to Species Availability 2009

To better understand changes in the patterns of primate vulnerability at RDS, we compared the relative primate species representation in hunter off-take in 2009 as reported by 15 hunters in 34 weekly surveys ($n = 793$ hunts surveyed, 906 primates reported) to the relative proportion of primate species observed on wildlife transects in that same year. Although hunters captured *L. albigena* in proportion to its availability, *C. nictitans* may have been hunted less than expected based on its high encounter rates on transects. Hunter off-take data also included rarer species that were not detected along transects. Thus, the off-take differed from expected based on the relative availability of primates observed along transects (G test of goodness of fit: $G = 42.02$, $\text{df} = 12$, $P \leq 0.001$). Further, males and females were not equally represented in the off-take reports, supporting hunters' claims that they targeted males more frequently than females (proportion of off-take male vs. female for each of seven species hunted (G test of goodness of fit: $G = 27.64$, $\text{df} = 6$, $P \leq 0.001$) (Table II). The single exception is *C. cephus*. In this species, females and males were almost equally targeted, perhaps consistent with their use of the understory, or the lack of active antipredator calling by *Cephus* males that may disproportionately increase hunter detection of the males of the other species (Fig. 4).

TABLE II. Percent Representation of Individual Adult Male and Female Monkeys in Hunter Off-Take Surveys at RDS in 2009

	C. pogonias	*C. cephus*	*C. nictitans*	*C. neglectus*	*L. albigena*	*C. agilis*	*C. guereza*	*P. badius*	Total
Total	39	129	317	17	253	86	35	0	906
Male	59% (23)	40% (51)	81% (258)	94% (16)	67% (170)	64% (55)	83% (29)	– (0)	66% (602)
Female	41% (16)	60% (78)	19% (59)	6% (1)	33% (83)	36% (31)	17% (6)	– (0)	34% (304)

(n) = number of individuals.

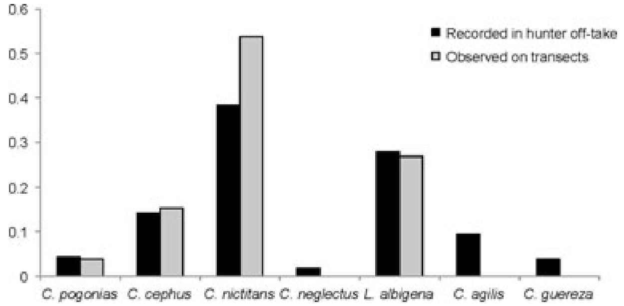

Fig. 4. A comparison of the proportions of monkey species observed in hunter off-take relative to the presence of monkey groups on transects at RDS, 2009. *Procolobus badius* is not included as it was neither present in hunter off-take nor on transects. However, data collected ad libitum with hunters in Bayanga demonstrate that *P. badius* are hunted in other areas of RDS.

Comparisons to other Studies

Longer term changes in primate abundance at RDS 1994–2009

When we extended our analysis to include results from previous studies to compare primate abundance (observations/ km) along transects in four study periods, we found significant declines over time 1994–2009 (Kruskal–Wallis test for independent samples 1994, 1999, 2002, and 2009: Total monkey groups observed/km: H = 18.684, df = 3, $P \leq 0.001$; *L. albigena* groups/km: H = 24.937, df = 2, $P \leq 0.001$; *C. agilis* groups/km: H = 9.823, df = 2: $P \leq 0.007$; *C. nictitans* groups/km: H = 13.26, df = 2, $P \leq 0.001$; *C. cephus* groups/km: H = 10.21, df = 3, $P \leq 0.017$; *C. pogonias* groups/km: H = 23.801; df = 3, $P \leq 0.001$) [Noss, 1995; Shah, 2003] (Table I).

There were few differences in primate abundance along transects in the park between the 1999/2001 (0.87 groups/km) and 2002 (1.13 groups/km) study periods. While monkeys do not appear to have been targeted in either remote Mondika or busier Dzanga Park or adjacent reserve before 2002, by 2009 there was a discernable drop in primate abundance in the Dzanga Park (0.25 monkey groups/km). Observations of monkeys in the Reserve have declined over time (1994 = 0.34 monkey groups in reserve/km; 2002 = 0.53 monkey groups in reserve/km, 2009 = 0.18 monkey groups in reserve/km) (Table I).

Primate community composition at RDS 1986–2009

Primate community composition (relative species representation on transects) at RDS varied between study periods in our broadest comparison, 1986–2009 (G test of goodness of fit: $G = 165.98$, df = 30, $P \leq 0.001$, Table III). The presence of *C. nictitans*, relative to the other species, has fluctuated across study periods and sectors but generally increased over time. At RDS, both the red colobus and the black and white colobus have been rare compared to other African sites [Chapman et al., 2010; McGraw, 2007]. This has been the case since the earliest primate surveys at RDS in 1986, when red colobus was only occasionally found in swampy areas [Fay, 1989]. Black and white colobus at RDS have typically been encountered in swampy, riverine areas, or in salines, and only rarely encountered in mixed-species forest. We occasionally observed *C. neglectus* near the Sangha river in 2009, but did not detect it on our 2002 or 2009 transects reported here. *Allenopithecus* has been purported to be present by local hunters with strong knowledge of primates [Blom et al., 2005], but has never been seen along transects at RDS. However, the ethnographic data supported their presence as 87% of hunters interviewed reported the presence of “simbi,” the “monkey of the swamp,” which they noted was readily differentiated from the white-bearded DeBrazza’s monkey.

DISCUSSION

This study suggests that human hunting pressures and changing hunting technology have had a greater effect on monkey species at RDS than any negative outcomes of logging. The combination of market data and ethnographic interviews allowed us to interpret changing patterns of primate abundance and behavior on RDS transects over time. Declining observation encounter rates at our three main transect sites between 2002 and 2009 indicated that monkey species had declined in both park and reserve. These declines were coupled with reductions in primate vocalization encounter rates, suggesting the adoption of cryptic antipredator strategies and declines in primate numbers. The combination of ecological line-transect data with

TABLE III. Primate Community Composition at RDS: Changes in Proportions of Monkey Group Observations on Transects Over Time, 1986–2009

Year of study (number transects)		Species							
	Total km Total group observations	*C.pogonias*	*C.cephus*	*C.nictitans*	*C.neglectus*	*L.albigena*	*C.agilis*	*C.guereza*	*P.badius*
1986 (2) Fay (1989)	214 km 52 obs	0.230	0.115	0.270	0.000	0.270	0.000	0.058	0.058
1994 (6) Noss (1995)	93 km 93 obs	0.075	0.161	0.667	0.000	0.032	0.0140	0.000	0.000
1997 (18)	81.8 km 14 obs	0.000	0.143	0.286	0.000	0.571	0.000	0.000	0.000
1999 (1) Shah (2003)	195 km 173 obs s	0.100	0.176	0.353	0.000	0.318	0.035	0.012	0.000
2002 (20)	410 km 288 obs	0.160	0.181	0.43	0.024	0.139	0.024	0.007	0.000
2009 (20)	105.4 km 26 obs	0.038	0.154	0.538	0.000	0.269	0.000	0.000	0.000

km = total kilometers surveyed; obs = total number of sightings on transects.

ethnographic and market inquiries further supported the idea that monkeys in RDS have experienced both populations declines and changes in behavior. Moreover, increases in gun hunting intensity made monkeys a more common target for hunters while also causing them to become more cryptic in those areas under the highest hunting pressure [Daspit, 2011; Jost Robinson et al., 2011].

Apparent declines in monkey populations at RDS are still confounded by the potential that monkeys hide or use substrates differently in hunted forests. However, the increasing numbers of monkeys documented in surveys of hunter off-take confirmed that monkeys' adoption of new antipredator strategies have been largely unsuccessful at RDS. We suggest that future studies might expand data collection on transects to include variables often collected for behavioral primate field studies. Adding variables such as animal height in trees, substrate use, and nearest neighbor distances would have allowed us to better detect changing behavioral responses of primates to hunters.

The larger bodied and most vocal species, *C. nictitans* and *L. albigena*, were the most hunted of the primates, and appeared on a daily basis in the market at Bayanga in 2009 [Daspit, 2011; Jost Robinson et al., 2011]. These two species were rare on transects at the sites where human activity and hunting pressure were particularly intense. Monkeys have become important targets of hunters in the region, though they were still less-frequently captured during the study than duikers [Eves & Bakarr, 2001]. In 2002, we had found little evidence of discernable poaching sign influencing monkey numbers in the reserve where densities were already low. However, in the park where densities were higher in 2002, poaching activity was becoming more apparent and monkeys had declined relative to earlier studies. By 2009, monkey abundance in the park had fallen to approach the low numbers in the reserve suggesting similar levels of hunting pressure for monkeys between park and reserve by that time. The ethnographic data and information about the increasing use of guns in the reserve area allowed us to document the transition to greater hunting of primates alongside of their greater vulnerability and declining abundance in both the reserve and the park.

Ecological Flexibility in Primate Communities at RDS

Behavioral plasticity and life history traits of hunted wildlife have been shown to influence extant mammal assemblages in African forests, suggesting species variability in resistance to hunting [Oates 1996; Struhsaker, 1999]. van Vliet & Nasi [2008] noted that smaller terrestrial species such as blue duikers and the African brush-tailed porcupine were more resistant to hunting pressure than small monkeys. However at Korup, Cameroon and Tai Forest, Cote d'Ivoire, particular primate species seemed at least temporarily resilient in the face of hunting pressures. Their persistence may relate to flexibility in habitat use, foraging, and antipredator strategies [Linder, 2008; Linder & Oates, 2011; McGraw, 2007].

While competition between species of nonhuman primates is particularly difficult to demonstrate without in situ experimentation, it may be possible to use changes in the relative abundance of species diversity over time as an indicator of density compensation or competitive exclusion [Linder & Oates, 2011; Peres & Dolman, 2000]. Our examination of monkey species represented on RDS transects from 1986 to -2009 indicated that *C. nictitans* had steadily increased in relative presence over time, while most other species had declined. *Cercopithecus nictitans* may be quite flexible in use of multiple types of habitats and across gradients of disturbance including agricultural mosaic and selectively logged forests. The Noss [1995] data from a disturbed RDS site show *C. nictitans* was particularly prevalent in that forest edge before gun hunting was common at RDS (Table III).

Data from other sites indicate that *C. nictitans* is typically highly insectivorous and capable of exploiting agricultural mosaic and logged forest areas [Baya & Storch, 2010; Chapman et al., 2002; McGraw, 2007], whereas *L. albigena* may be generally more dependent on a narrower range of foods, especially seeds [Gautier-Hion et al., 1980; Ham, 1994]. At Mondika, Shah [2003] pointed to the strong dependence of *L. albigena* on *Erythrophleum suavolens* [also Poulsen et al., 2005]. *Lophocebus albigena* has been well represented at RDS and it appeared to have been relatively resistant to hunting in 2002, but its abundance has been consistently lower than *C. nictitans* at all disturbed sites since guns have become common. *Lophocebus albigena* may have been disproportionately hunted relative to their abundance at RDS given their antipredator strategies that included loud calls and mobbing, which made adult males particularly susceptible to human hunters. Linder & Oates [2011] have also reported increases in the relative occurrence of *C. nictitans* at Korup and suggested that it has benefited from competitive release as drills and red colobus became rarer over time. Further study of the factors that could limit the ability of *C. nictitans* to use exploited habitats would be useful for recommendations for the development of active hunting management plans.

Overall, the largest, most common monkey species are those most targeted by hunters at RDS. Yet, transect data and indices of hunting tolerance in conjunction with ethnographic data demonstrate that size and profit are not the only drivers of prey choice. It is not clear whether the recent low representation of colobines at RDS results from longer term hunting pressure on these large primates. Red colobus was cited in interviews with indigenous populations as a favorite food, yet hunters attributed childhood illnesses, specifically epilepsy, to the consumption of *C. guereza*. In any case, low abundance of colobines does not appear to be a direct result of logging. Colobines are rare in both logged northern and unlogged southern regions of RDS and black and white colobus are usually reported to do well in lightly logged areas [Chapman et al., 2010; Struhsaker, 1997], unless subject to heavy predation by chimpanzees [Lwanga et al., 2011].

Recent fluctuations in the relative distribution of *L. albigena* and *C. nictitans* at RDS may have been more likely influenced by recent human hunting pressure as these are the largest and among the more common primate species at RDS, appearing most often in hunter off-take surveys and for sale in local bushmeat markets. Additionally, most hunters in our sample reported *C. nictitans* to be the most preferred of monkeys species in RDS followed by *L. albigena*.

Our data further point to the importance of fluctuations in human populations and loss of traditions influencing prey choice at RDS. Previous to 2002, *C. pogonias* was relatively resistant to hunting pressure, consistent with feeding taboos documented in RDS and other sites [see Kumpel, 2006]. However, more recently this species appeared to have lost its tolerance to hunting, likely the result of increased hunting pressure from growing human populations and shifting hunting technologies. Given its relatively small size, we posit that *C. pogonias* have recently become a target of nonlocal hunters because of the erosion of cultural taboos related to the changing composition of local human populations at RDS.

What is the Future for Primate Assemblages in Exploited Forests?

Recent work at Korup and at RDS suggests that human exploitation influences the diversity of persisting primate assemblages. Some primate species are able to take advantage of new resources in agricultural margins or selectively logged forests; some even appear at least temporarily resilient to hunting pressure. However, this research illustrates that even in protected areas, primates are vulnerable to local extirpation once hunting pressure escalates following the widespread introduction of arms. If hunting prohibitions do not function more effectively in managed or protected regions, primate assemblages are likely to continue to shrink throughout the forests of central and West Africa.

Our long-term efforts to monitor primate populations at RDS and to integrate quantifiable measures of hunting and habitat heterogeneity [see also Rist et al., 2009] have provided us an opportunity to assess the relative importance of hunting and logging while acknowledging the synergistic nature of these impacts in Central African sites [also Waltert et al., 2002]. Surveys are designed to quickly evaluate primate abundance. However, surveys can also be used as a rapid assessment of behavioral changes in prey species in regions where longer studies are logistically difficult or cost-prohibitive. At RDS, monkeys have become quiet in hunted areas, suggesting behavioral changes in response to increasing human activity and gun hunting in the reserve. Hunters at RDS have responded to declines and cryptic behavior in the reserve by shifting to focus on gun hunting in the park. Thus, although many primates at RDS exhibit flexibility in their use logged forests and show behavioral adaptations to reduce their vulnerability to hunting, these changes appear unable to keep pace with hunter counterstrategies and the large-scale encroachment of arms and people into Central African forests.

ACKNOWLEDGMENTS

This research complied with PACUC regulations (Protocol 98-047 and 08-021) and the laws of the Central African Republic. We thank the government of the Central African Republic and the RDS Project for permission to conduct this research and the support of WWF staff and our research team, especially Wonga Emile, and the tracking teams, Bruno Bokoto DeSemboli, Jennifer Cooper, Jean Bosco Kpanou, Jean Bernard Dickey, Eugene Mbea, and the late Carolin Sambo.

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