Impacts of Roads and Hunting on Central African Rainforest Mammals

WILLIAM F. LAURANCE,* BARBARA M. CROES,† LANDRY TCHIGNOUMBA,† SALLY A. LAHM,†‡ ALFONSO ALONSO,† MICHELLE E. LEE,† PATRICK CAMPBELL,† AND CLAUDE ONDZEANO†

*Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panamá, email laurancew@si.edu

†Monitoring and Assessment of Biodiversity Program, National Zoological Park, Smithsonian Institution, P.O. Box 37012, Washington, D.C. 20560–0705, U.S.A.

‡Institut de Recherche en Ecologie Tropicale, B.P. 180, Makokou, Gabon

Abstract: *Road expansion and associated increases in hunting pressure are a rapidly growing threat to African tropical wildlife. In the rainforests of southern Gabon, we compared abundances of larger (>1 kg) mammal species at varying distances from forest roads and between hunted and unhunted treatments (comparing a 130-km² oil concession that was almost entirely protected from hunting with nearby areas outside the concession that had moderate hunting pressure). At each of 12 study sites that were evenly divided between hunted and unhunted areas, we established standardized 1-km transects at five distances (50, 300, 600, 900, and 1200 m) from an unpaved road, and then repeatedly surveyed mammals during the 2004 dry and wet seasons. Hunting had the greatest impact on duikers (*Cephalophus spp.*), forest buffalo (*Syncerus caffer nanus*), and red river hogs (*Potamochoerus porcus*), which declined in abundance outside the oil concession, and lesser effects on lowland gorillas (*Gorilla gorilla gorilla*) and carnivores. Roads depressed abundances of duikers, sitatungas (*Tragelaphus spekei gratus*), and forest elephants (*Loxondonta africana cyclotis*), with avoidance of roads being stronger outside than inside the concession. Five monkey species showed little response to roads or hunting, whereas some rodents and pangolins increased in abundance outside the concession, possibly in response to greater forest disturbance. Our findings suggest that even moderate hunting pressure can markedly alter the structure of mammal communities in central Africa. Roads had the greatest impacts on large and small ungulates, with the magnitude of road avoidance increasing with local hunting pressure.*

Keywords: Gabon, infrastructure, oil development, rainforest, tropical forests, wildlife conservation

Impactos de Carreteras y Cacería sobre Mamíferos de Bosque Lluvioso en África Central

Resumen: *La expansión de carreteras asociada con incrementos en la presión de cacería son una amenaza creciente para la vida silvestre tropical Africana. En los bosques lluviosos del sur de Gabón, comparamos las abundancias de especies de mamíferos mayores (>1 kg) a diferentes distancias de las carreteras y entre tratamientos con y sin cacería (comparamos una concesión petrolera de 130 km² que estaba casi totalmente protegida de la caza con áreas cercanas afuera de la concesión que tenían presión de caza moderada). En cada uno de los 12 sitios que estaban repartidos equitativamente en áreas con caza y sin caza, establecimos transectos estandarizados de 1 km a cinco distancias (50, 300, 600 900 years 1200 m) de un camino no pavimentado, y muestreamos mamíferos repetidamente durante las estaciones seca y lluviosa de 2004.La cacería tuvo el mayor impacto sobre duikers (*Cephalophus spp.*), búfalo de bosque (*Syncerus caffer nanus*) y *Potamochoerus porcus*, cuya abundancia declinó afuera de la concesión petrolera, y menos efectos sobre gorilas (*Gorilla gorilla gorilla*) y carnívoros. Los caminos deprimieron la abundancia de duikers, sitatungas (*Tragelaphus spekei gratus*) y elefantes (*Loxondonta africana cyclotis*), la evasión de caminos fue mayor afuera que adentro de la concesión. Cinco especies de monos no mostraron respuesta a los caminos o a la cacería, mientras que la abundancia de algunos roedores y pangolines aumentó afuera de la concesión, posiblemente*

Paper submitted June 20, 2005; revised manuscript accepted September 21, 2005.

Conservation Biology Volume **, No. *, ***–***

DOI: 10.1111/j.1523-1739.2006.00420.x

en respuesta a una mayor perturbación del bosque. Nuestros resultados sugieren que aun la cacería moderada puede alterar significativamente la estructura de comunidades de mamíferos en África central. Las carreteras tuvieron los mayores impactos sobres ungulados grandes y pequeños, la magnitud de la evasión de caminos aumentó con la presión de cacería local.

Palabras Clave: Bosque lluvioso, bosques tropicales, conservación de vida silvestre, desarrollo petrolero, Gabón, infraestructura

Introduction

African tropical rainforests are a key global conservation priority because of their high biological uniqueness and rapid rates of forest loss and degradation (Olson & Dinerstein 1998; Kamdem-Toham et al. 2003). Rainforests in West and East Africa have been reduced to just 8–12% of their former extent (Naughton-Treves & Weber 2001). Central African rainforests, including the vast Congo Basin, still encompass nearly 60% of their original distribution, but are being increasingly threatened by escalating human population growth, industrial logging, slash-and-burn farming, road and infrastructure expansion, and overhunting (Naughton-Treves & Weber 2001; Wilkie & Laporte 2001).

Hunting pressure is growing rapidly throughout central Africa, as road networks expand and the area of forest accessible to hunters increases (Wilkie et al. 1992; Barnes et al. 1997; Fa et al. 2005). Moreover, the efficiency of hunters has increased because shotguns and cable snares have replaced traditional crossbows, spears, and nets (Lahm 1993*a*, 2001; Noss 1998). Wild meat is a key protein source in rural areas and is favored in towns and cities. These factors drive a burgeoning commercial bushmeat trade (Lahm 1991*a*, 1993*b*; Milner-Gulland et al. 2003). Of 57 mammal, bird, and reptile species hunted in the Congo Basin, 60% are being exploited unsustainably (Fa et al. 2002). In parts of West Africa, chronic overhunting and forest loss has led to a near collapse of the bushmeat trade and the possible extinction of a primate species (Oates et al. 2000). The total harvest of wildlife in the Afrotropical region is estimated to be 1–5 million tons annually, making it one of the most intensively hunted tropical regions in the world (Wilkie & Carpenter 1999; Fa et al. 2002).

Fortunately, the nation of Gabon has partially escaped the acute environmental pressures plaguing other Central African countries. Favored with substantial oil and mineral deposits and rich timber resources, the country has enjoyed a relatively high degree of political and social stability and a per-capita income that is four to six times higher than most other sub-Saharan countries (CIA 2004). Moreover, much of Gabon's forest—among the richest and most biologically important in Africa—is still largely intact, and for this reason is likely to play a key role in regional conservation strategies (Kamdem-Toham et al. 2003; Alonso et al. 2006; Laurance et al. 2006).

Nonetheless, in coming years Gabon and its forests will face serious challenges. The country's greatest near-term economic problem is that its petroleum reserves are rapidly declining (Trebaol & Chaillol 2002). As oil revenues have fallen, the Gabonese government has become increasingly reliant on timber exports (Berre 1998), leading to a dramatic growth in logging. Today, timber concessions (long-term timber leases) encompass 45% of the country's land area and two thirds of its remaining forest (Collomb et al. 2000). Logging promotes encroachment by slash-and-burn farmers (Laurance 2001) and increases commercial and subsistence hunting by providing hunters with greater access to unexploited wildlife populations (Robinson et al. 1999), lowering the cost of transporting bushmeat to market (Wilkie et al. 1992, 2000; Lahm 1993*b*), and increasing incomes of local consumers (Wilkie et al. 2005).

We assessed the effects of roads and hunting on rainforest mammals in southern Gabon. Our study offers some important advantages over earlier published investigations of hunting in this region. First, it is focused on a diverse assemblage of species—monkeys, apes, small and large ungulates, carnivores, and semifossorial species—rather than just a single species (e.g., Barnes et al. 1991, 1997; Lahm et al. 1998; but see Lahm 1993*b* for a comprehensive unpublished study). Second, our study was rigorously designed and replicated and included an experimental control area (a large oil concession) that was almost entirely protected from hunting. This design allowed us to quantitatively assess the relative effects of roads and hunting (and their interaction) on different species and guilds of mammals. Finally, our project has both general and key local relevance, because the study area is a potentially critical corridor between two recently designated national parks in Gabon, and its future is far from secure.

Methods

Study Area

Our study area in southwestern Gabon (1° 55′ S, 9° 50′ E) encompassed about 400 km^2, of which 130 km^2 was the Rabi oil concession, the highest-producing onshore oilfield in sub-Saharan Africa, operated by Shell-Gabon Corporation since 1985. Annual oil production at Rabi peaked at 88 million barrels in 1997 (60% of Gabonese oil production) but has since fallen to 20 million barrels, due to declining oil reserves (Trebaol & Chaillol 2002). The study area is an important forest corridor between two recently gazetted national parks, Loango (1550 km^2) to the west, and Moukalaba-Doudou (4500 km^2) to the east (Alonso et al. 2006).

The Rabi region is dominated by lowland tropical rainforest. Annual rainfall averages about 2300 mm and is highly seasonal, with dry seasons from June to October and from mid-December to mid-January, although most trees are evergreen because the driest months are cool and cloudy. The terrain is undulating, with rainforest on hills and slopes and seasonally inundated forest or swamps in gullies (de Bie & Geerling 1989). This sparsely populated area (<0.2 inhabitants/km^2) has only scattered villages and logging camps within 30 km of the oil concession. Prior to establishment of the oil field in the 1980s, much of the Rabi area was selectively logged (the old logging roads are mostly overgrown and impassable to vehicles), and field crews conducted extensive seismic surveys during oil exploration (Trebaol & Chaillol 2002).

Access to Rabi is strictly regulated by Shell-Gabon, which maintains guard posts at all access points. Several hundred oilfield workers are stationed at Rabi, but they are not allowed to leave the field camps at night, and their family members are not permitted inside the concession. Hunting and possession of firearms, snares, and bushmeat are forbidden, and security personnel search visitors' bags before they leave the concession. By Gabonese standards, workers are highly paid and have strong incentives not to hunt, given that they are well fed in company cafeterias and face immediate dismissal for hunting or transporting wildlife products. Speed limits (40 km/hour) are enforced for all vehicles. Efforts have also been made to minimize deforestation, replant some deforested areas, and regulate roadwork. Despite an extensive network of unpaved roads, numerous small (usually <2 ha) clearings for wellheads, and larger clearings for field camps, infrastructure, and an airstrip, about 90% of the original forest cover has been maintained inside the Rabi concession.

Outside the concession, conditions are somewhat different. Selective logging and oil operations are ongoing in several areas, where forest damage is heavier and more recent. Although the density of permanent roads is lower than inside the concession (Fig. 1), roads tend to be wider (see below). The human population within a 20-km radius of Rabi is sparse, averaging around 0.2 residents/km^2 (Trebaol & Chaillol 2002) in scattered villages and logging camps that range from a few to a few dozen families. Residents are members of bantou tribes who practice swidden farming, hunting, and fishing, and are sometimes employed by logging and oil companies (Lahm & Tezi 2006). Mosaics of farming plots and regrowth often occur within 1–2 km of villages. Because of the sparse human population, hunting pressure is generally light to moderate in a buffer just outside the concession and most intense within several kilometers of villages and roads. The expansion of roads from oil and logging activities facilitates some commercial hunting, with bushmeat being sold openly in regional towns such as Gamba and Tchibanga (Trebaol & Chaillol 2002).

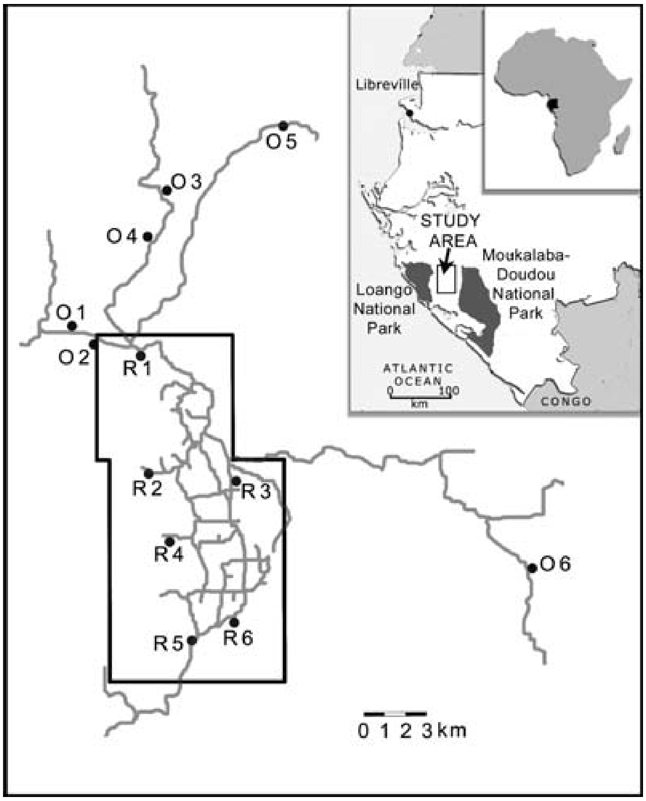

Figure 1. Map of the study area in southwestern Gabon, showing locations of study sites within the Rabi oil concession (sites R1–R6), where hunting is prohibited, and outside the concession (sites O1–O6), where hunting pressure is generally moderate. Wavy gray lines indicate roads, and the black line shows the boundary of the Rabi concession. Some roads outside the concession are not shown.

Study Sites

We used a stratified random design to select 12 study sites, half inside and half outside Rabi oil concession. Initially, 26 potential sites (15 inside and 11 outside the concession) were identified based on 1:25,000 maps, and then surveyed on foot. Potential sites were not extensively flooded, had a relatively straight road, and had no other active roads or clearings nearby. Sites outside the concession were all <6 km from a small village or logging camp, and were dominated by mature forest with little if any secondary regrowth or farming plots. Two sites were randomly selected from each of the northern, central, and southern parts of Rabi concession. Outside the concession, 1–2 sites were randomly chosen along each of four roads located to the northwest, north, northeast, and southeast of the concession. All sites were at least 2.4 km apart.

Mammal abundances were estimated using standardized transects, an effective technique in African rainforests (Koster & Hart 1988; Whitesides et al. 1988; Lahm 1993*b*). At each study site, we established five 1-km-long linear transects parallel to the road at distances of 50, 300, 600, 900, and 1200 m from the road (Fig. 1). We cut narrow trails along each transect with machetes, divided each transect into 20 segments (each 50 m long), and marked the divisions with flagging tape. Following trail cutting, all sites were left undisturbed for at least 3 weeks before commencing mammal censuses.

Census Methods

The 12 sites (60 transects) were censused twice in the dry season (July–August) and twice in the wet season (November–mid-December) in 2004, with at least 2-week intervals between successive censuses of any site. All censuses were conducted during daytime by a three-person team, two of whom were Gabonese with hunting experience and knowledge of local animal signs. The three observers walked transects slowly in single file, stopping frequently to scan in all directions with binoculars. Much care was taken to minimize noise from observers. The first observer searched for animal signs at ground level (e.g., footprints, diggings, dung, disturbed vegetation), the second recorded data and scanned for animal signs at eye level and above (e.g., ape nests, rubbing posts), and the third used visual, acoustic, and odor cues to search for nearby animals.

Many species could be identified based on their signs. However, three types of signs could not be used to discriminate among similar species (scientific names provide in Table 1): (1) footprints and dung of medium-sized duikers, (2) diggings of pangolins and larger rodents, and (3) very old nests of large apes (chimpanzees and gorillas). For these signs, the general categories above were recorded.

Each site required 1 full day to be censused. Censuses began at about 0700 hours and ended in late afternoon. During the first census at each site, observers began with the transect closest to the road and then moved to transects progressively farther from the road. On the next census of that site, the sequence of transects was reversed. This eliminated any systematic bias between time of day (which might influence animal activity) and distance from roads. We also alternated each census between sites inside versus outside the oil concession, to eliminate systematic variation in weather between hunted and unhunted treatments.

Table 1. Pearson correlations of mammal species (or groups of similar species with indistinguishable animal signs) in Gabon with two ordination axes.

Common name	*Scientific name*	*Axis 1*[a]	*Axis 2*[a]
Water chevrotain	*Hyemoschus aquaticus*	−0.287	0.051
Blue duiker	*Cephalophus monticola defriesi*	−0.289	−0.428*
Medium-sized duikers[b]	see below	−0.531*	−0.593*
Yellow-backed duiker	*C. silvicultor*	−0.349	−0.305
Sitatunga	*Tragelaphus spekei gratus*	−0.189	0.239
Forest buffalo	*Syncerus caffer nanus*	−0.137	0.016
Red river hog	*Potamochoerus porcus*	−0.046	−0.642*
African forest elephant	*Loxondonta africana cyclotis*	−0.855*	−0.148
Grey-cheeked mangabey	*Lophocebus albigena albigena*	−0.173	0.116
Red-capped mangabey	*Cercocebus torquatus*	−0.313	0.052
Crowned monkey	*Cercopithecus pogonias nigripes*	−0.095	0.066
Moustached monkey	*C. cephus cephodes*	0.119	−0.023
Putty-nosed monkey	*C. nictitans nictitans*	−0.020	0.123
Chimpanzee	*Pan troglodytes troglodytes*	0.089	0.011
Western lowland gorilla	*Gorilla gorilla gorilla*	−0.218	−0.035
Giant pouched rat	*Cricetomys emini*	0.270	−0.115
Brush-tailed porcupine	*Atherurus africanus centralis*	0.611*	0.740
Rodent and pangolin diggings[c]		0.152	0.693*
Variation explained (%)[d]		55.4	33.1

[a]*Significant correlations are indicated by asterisks. A Bonferroni correction (*p = *0.0042) was used to reduce the likelihood of spurious correlations.*

[b]*Includes five duiker species (Ogilby's,* Cephalophus ogilbyi crusalbaum*; Peter's,* C. callipygus callipygus*; black-fronted,* C. nigrifons nigrifons*; white-bellied,* C. leucogaster*; and bay,* C. dorsalis castaneus*) whose footprints and dung could not be distinguished.*

[c]*These were likely made by the brush-tailed porcupine, giant pouched rat, marsh cane-rat (*Thryonomys swinderianus*), giant pangolin (*Smutsia gigantea*), and tree pangolin (*Phataginus tricuspis*).*

[d]*Coefficients of determination for correlations between ordination distances and distances in the original* n*-dimensional space.*

To generate standardized estimates of species abundances, we determined the number of 50-m segments on each 1-km transect in which a species or its sign was detected. This yielded a 0–20 score for each species. Data from the four censuses were then pooled to yield an average value on each transect for each species. For each of five monkey and mangabey species (Table 1) that were commonly seen and counted, we also generated an abundance estimate based on the total number of individuals observed per transect. Results from this analysis were very similar to that obtained for our 0–20 abundance score, so we report only the latter here.

Hunting and Habitat Data

We derived an index of hunting pressure for each transect based on snares, human footprints, machete cuts, spent gun cartridges, hunting camps, encounters with hunters, and butchered animal carcasses encountered along the transect or on gunshots heard nearby (0, no evidence of human activity; 1, evidence of prior activity; 2, evidence of current activity, such as active snares, recent machete cuts, or gunshots). Data on hunting pressure were collected throughout the study.

In addition, for every 50-m segment along each transect, we collected data on five habitat variables: (1) percentage of the ground surface that was swampy or inundated (0 = none, 1 = 1–25, 2 = 26–50, 3 = 51–75, 4 = 76–100%); (2) understory-vegetation density (1, low; 2, moderate; 3, high); (3) canopy cover (1, <50%; 2, 50–75%; 3, >75% cover); (4) logging damage, based on old logging tracks or cut stumps (1, none; 2, light; 3, heavy or recent); and (5) topography (1, gully bottom; 2, lower slope; 3, upper slope; 4, ridgetop/plateau). Habitat data were collected during the dry season, and all values were averaged for each transect. Finally, at each of the 12 study sites, we measured the width of the road clearing (including verges) at 100-m intervals ($n = 11$ measurements per site).

Data Analysis

We quantified mammal assemblages in three ways. First, species-level analyses were conducted for the most abundant species (see Table 1 and below for scientific names of species). Second, species were pooled into six functional guilds: (1) monkeys (including mangabeys), (2) apes (gorilla and chimpanzee), (3) smaller ungulates (duikers and water chevrotain), (4) large ungulates (sitatunga, forest buffalo, red river hog, forest elephant), (5) carnivores (leopard [*Panthera pardus pardus*], African civet [*Civettictis civetta*], genet [*Genetta* sp.], unknown mongoose species), and (6) semifossorial species (rodents and pangolins that frequently dig or burrow while foraging). Third, nonmetric multidimensional scaling, an ecological ordination technique (McCune & Mefford 1999), was used to identify major gradients in species abundances across our study area. For this analysis, we used raw data on sightings and signs of species (0–20 scale), excluding rare species (detected at <20% of transects), with Sorensen's distance metric. Randomization tests ($n = 50$) were used to determine the number of ordination axes that explained significantly more variation than expected by chance.

We used analyses of covariance (ANCOVAs) to test the effects on mammals of the hunting "treatment" (inside vs. outside Rabi concession) and of distance to roads (used as a covariate). The best subsets and multiple regressions were also used to identify combinations of environmental variables (hunting pressure, distance to road, logging, canopy cover, understory cover, topography, soil inundation) that influenced mammal abundances. Species abundance and habitat data were log transformed as needed to reduce heteroscedasticity and improve normality.

Results

Hunting and Habitat Variables

Fifty-six percent of all transects outside Rabi oil concession had signs of nearby hunting activity (e.g., human footprints, machete cuts, shell casings) versus just 6% of transects inside the concession. Hunting pressure was significantly higher outside than inside the concession ($p < 0.001$) but did not vary significantly as a function of distance to roads ($p = 0.92$; ANCOVA). Among all 12 study sites, average hunting pressure (mean score for all transects) was strongly and negatively correlated with distance to the nearest village or logging camp ($r_s = -0.897$, $p = 0.00008$; Spearman rank correlation).

In addition to hunting, study sites inside and outside the concession differed in several respects. Road clearings were typically wider outside (mean ± SD = 27.3 ± 8.6 m) than inside (18.8 ± 4.0 m) the concession ($t = 2.29$, df = 10, $p = 0.045$; t test with log-transformed data). In addition, sites outside the concession had significantly heavier logging ($p = 0.0002$), reduced canopy cover ($p = 0.02$), and heavier understory cover ($p = 0.002$), whereas no habitat variables were significantly influenced by distance to roads ($p > 0.05$ in all cases). Topography and soil inundation did not differ significantly in any comparison (all ANCOVAs).

Ordination of Mammal Communities

Eighteen species (or groups of similar species indistinguishable from their signs; see Table 1) were included in the ordination analysis. Two ordination axes captured most of the variation in the data set. Axis 1, which explained 55% of the total variation, described a gradient between transects with many forest elephants and medium-sized duikers and those with many brush-tailed porcupines. Axis 2 explained 33% of the variation and described a gradient between transects with many red river hogs,

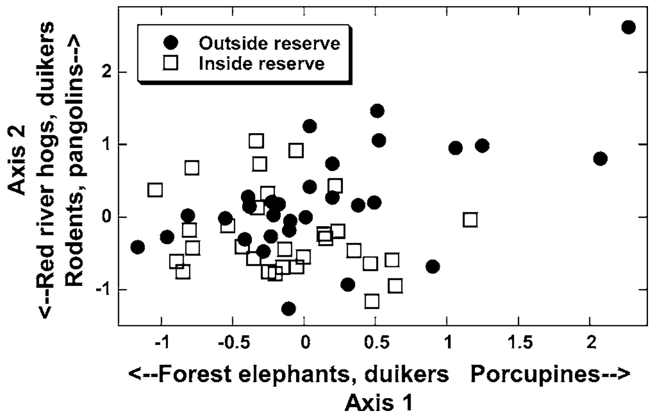

Figure 2. Ordination of rainforest mammal communities detected along 60, 1-km transects in southern Gabon. Axis lengths are proportional to the amount of variation explained by each axis.

medium-sized duikers, and blue duikers and those with many rodent and pangolin diggings (Table 1).

When the ordination scores were plotted (Fig. 2), transects outside the Rabi concession were generally skewed toward higher values on both axes, although the difference was significant only for axis 2 ($t = -2.64$, df $= 58$, $p = 0.011$; t test). This suggests that several duiker species and red river hogs declined in abundance outside the concession, whereas rodent and pangolin diggings increased.

Among our seven environmental predictors (hunting pressure, distance to roads, logging, canopy cover, understory cover, topography, soil inundation), distance to roads had by far the largest influence on axis 1 (Fig. 3a), although topography was also marginally significant (best-subsets regression). However, mammal-community responses to roads were much stronger outside ($F_{1,28} = 11.94$, $R^2 = 29.9\%$, $p = 0.002$) than inside the oil concession ($F_{1,28} = 2.33$, $R^2 = 7.7\%$, $p = 0.14$). Of these same variables, only hunting pressure (Fig. 3b) had a significant effect on axis 2 ($F_{1,58} = 13.80$, $R^2 = 19.2\%$, $p = 0.0005$; all linear regressions). Collectively, these results suggest that roads and hunting pressure both had a strong impact on mammal communities but that road avoidance (mainly by forest elephants and duikers) was much stronger in hunted than unhunted areas.

Guilds and Species

Analyses of mammal guilds and species were generally concordant with the ordination analysis (Table 2). Among the six guilds, roads had negative effects on small and large ungulates, whereas hunting negatively affected small ungulates and carnivores. Surprisingly, rodents and pangolins evidently responded positively to hunting, and large ungulates in general were positively associated with logging. Topography, understory cover, and soil inundation also influenced some guilds (Table 2).

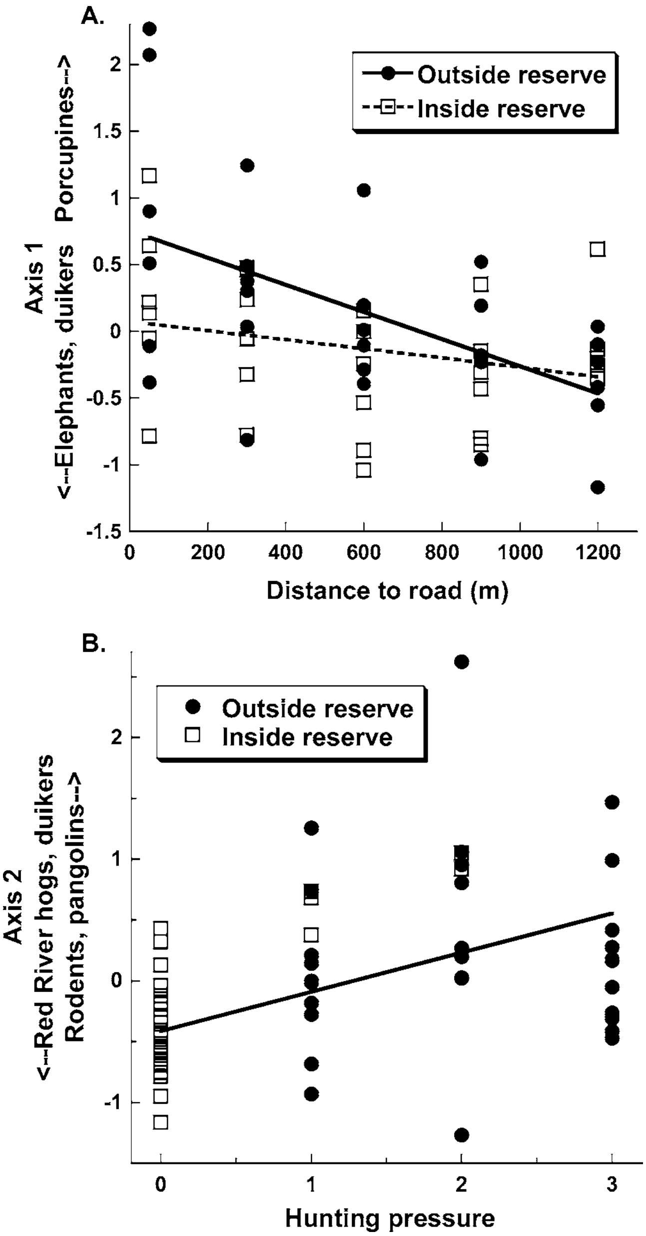

Figure 3. Effects of roads on scores for rainforest mammal communities for (a) ordination axis 1, and (b) ordination axis 2, contrasting patterns inside and outside an unhunted oil concession.

Among 15 relatively common species (or groups of similar species) detected on at least 20% of all transects, several trends were evident (Table 2). First, hunting had negative effects on a number of species, including medium-sized duikers, forest buffalos, red river hogs, and gorillas. Second, blue duikers, medium-sized duikers, and forest elephants responded negatively to roads (Fig. 4), and no species responded positively to roads. Third, topography significantly affected many ungulates (blue duikers, medium-sized duikers, yellow-backed duikers, forest buffalo, forest elephants), which invariably favored

Table 2. Predictors of the abundance of mammal guilds and relatively common species in Gabon based on analyses of covariance (ANCOVA) and multiple regressions.*

	ANCOVAs							
	concession effect		*road effect*		*Multiple regressions*			
	$F_{1,58}$	p	$F_{1,57}$	p	*predictors*	F	R^2 (%)	p
Group								
small ungulates	7.94	0.0067	17.61	0.0001	−topography −roads −hunting	18.30	49.5	<0.0001
large ungulates	0.17	0.68	18.12	0.0001	−roads +logging −topography	11.31	37.3	<0.0001
monkeys	0.07	0.79	0.56	0.46	—	—	—	—
apes	1.98	0.16	0.01	0.94	+understory	4.54	7.3	0.038
carnivores	1.52	0.22	0.68	0.50	−hunting	3.00	4.9	0.089
rodents/pangolins	3.13	0.082	0.10	0.92	+hunting −inundation	7.72	21.3	0.001
Species								
blue duiker	0.90	0.35	6.23	0.015	−topography −understory −roads	5.44	22.6	0.002
medium-sized duiker	8.21	0.006	15.56	0.0002	−topography −roads −hunting	4.86	20.7	0.005
yellow- backed duiker	3.97	0.051	5.36	0.024	−topography	21.16	26.7	<0.0001
sitatunga	0.01	0.91	3.89	0.054	+inundation	5.60	8.8	0.021
forest buffalo	5.52	0.022	0.24	0.62	−hunting −topography	3.39	10.6	0.041
red river hog	3.64	0.062	2.16	0.15	−hunting −understory	7.56	21.0	0.001
forest elephant	0.02	0.90	17.85	0.0001	−roads +logging −topography	10.58	36.2	<0.0001
gray-cheeked mangabey	0.44	0.51	1.23	0.27	−canopy	3.65	5.9	0.061
red-capped mangabey	0.00	0.95	0.12	0.73	−canopy −understory	3.06	9.7	0.055
crowned monkey	0.06	0.80	0.49	0.49	—	—	—	—
moustached monkey	0.03	0.86	0.78	0.38	—	—	—	—
putty-nosed monkey	0.00	0.95	0.42	0.52	—	—	—	—
chimpanzee	2.46	0.12	0.02	0.89	+understory	3.11	5.1	0.083
lowland gorilla	0.04	0.85	0.01	0.92	+understory −hunting	3.17	10.0	0.049
brush-tailed porcupine	6.46	0.014	0.31	0.58	+hunting	5.55	8.7	0.022

**"Concession effect" indicates the comparison between mammal populations inside versus outside the Rabi oil concession. For regressions, plus or minus signs show slopes of significant predictors (a negative slope for topography indicates the species favored gullies over ridgetops).*

wetter gullies and lower slopes over drier plateaus and ridgetops. Fourth, understory cover positively affected apes but negatively affected blue duikers, red river hogs, and red-capped mangabeys. Finally, monkeys were only weakly influenced by hunting, roads, and other habitat variables.

Discussion

Key Trends

Our findings suggest that even moderate hunting pressure can markedly alter the structure of rainforest mammal communities in tropical Africa (see also Fa et al. 2005). Relative to a no-hunting zone managed for intensive oil production, nearby areas outside the concession had significantly fewer duikers, forest buffalos, and red river hogs. Carnivores and gorillas also declined in the most heavily hunted areas outside the oil concession. Roads had significant negative impacts on duikers and forest elephants, with elephants showing much stronger road avoidance outside than inside the concession, presumably as a result of increased hunting activity near roads (Fig. 4). Such changes in mammal community structure can have potentially broad effects on forest ecosystems via alterations in predation, herbivory, and seed dispersal

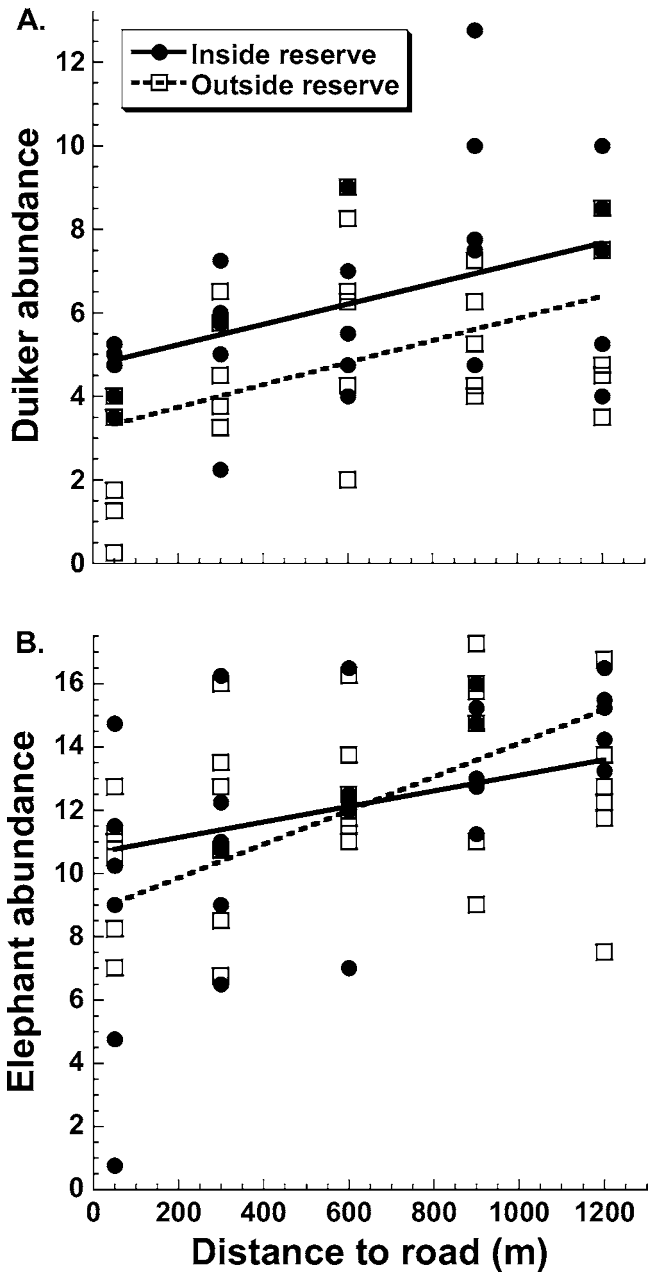

Figure 4. Abundance of (a) duikers and (b) forest elephants (0–20 scale) as a function of distance from roads inside and outside an unhunted oil concession.

(Roldán & Simonetti 2001; Wright 2003; Alonso et al. 2006; Laurance & Peres 2006).

It is important to emphasize that hunting intensity was not the only difference between the Rabi oil concession and nearby outside areas. Although both have similar topography and are largely dominated by old-growth rainforest, outside areas have a scattering of small villages and logging camps, mosaics of farming plots and regrowth near the villages, heavier and more recent logging disturbances that resulted in reduced canopy cover and denser understory cover, and typically wider roads than areas inside the concession. Some of these differences may have influenced our findings. For example, a possible explanation for increased numbers of rodents and pangolins outside the concession is that they may favor logged forest or agricultural mosaics, as has been shown for rodents elsewhere in Gabon and central Africa (Lahm 1991*a*, 1993*b*, 1994; Malcolm & Ray 2000). Among our 12 study sites, overall rodent and pangolin abundance increased closer to villages ($r = -0.557$, $p = 0.06$; Pearson correlation). Gorillas also favor mosaics of primary and regrowth forest (Tutin & Fernandes 1984; Lahm 1993*b*, 1994; White & Tutin 2001) and were once observed within 1 km of a small village, which might explain why gorilla numbers did not decline significantly outside Rabi concession despite the fact that gorilla abundance was negatively correlated with local hunting pressure. Some villagers in our study area and elsewhere in Gabon clearly do hunt and trap gorillas (Lahm 1993*b*; Lahm & Tezi 2006).

Hunting and roads not only caused important changes in mammal community structure, but also altered the behavior of many species. For example, when encountered by our team of observers, duikers, water chevrotains, and monkeys showed a much stronger propensity to flee outside than inside the oil concession (Croes et al. 2006). Could such differences in human-avoidance behavior affect the detectability of wildlife inside versus outside the concession? Such effects were probably of limited importance for small and large ungulates, carnivores, apes, rodents, and pangolins, which were most often detected from their footprints, dung, or other signs. Monkeys, however, were almost always detected acoustically, via their alarm calls. Nevertheless, the incidence of alarm calls did not differ appreciably between groups of monkeys encountered inside versus outside the concession (Croes et al. 2006); thus, our census results were probably influenced little by observed differences in animal behavior.

Potential Barrier Effects of Roads

Could the relatively narrow (usually <40 m wide) roads we studied act as a movement barrier to some species? Forest roads can significantly reduce local movements and alter the behavior of some rainforest fauna (Goosem 1997; Mason & Thiollay 2001; Lahm & Tezi 2006), such as certain understory birds (Develey & Stouffer 2001; S. G. Laurance et al. 2004), forest-interior bats (Soriano & Ochoa 2001), and strictly arboreal species (Johns 1992). Many of the mammal species we studied, however, are relatively large and are likely to have more coarse-grained habitat requirements than do small flying and arboreal vertebrates. During nighttime spotlighting censuses along roads, we observed many species—blue duikers, yellow-backed duikers, sitatungas, forest elephants, forest buffalos, red river hogs, marsh mongooses, African civets, palm civets, and leopards—at least occasionally traversing roads inside and outside the Rabi oil concession (W.F.L. and B.M.C., unpublished data). In addition, chimpanzees, gorillas, and all monkey species except the rare gray-cheeked mangabey were observed crossing roads during the daytime.

However, roads could be far more formidable barriers to strictly arboreal species, including the potto (*Perodicticus potto*), Thomas' galago (*Galagoides thomasi*), Demidoff's galago (*G. demidoff*), and Lord Derby's anomalure (*Anomalurus derbianus*), among others (S.A.L., W.F.L., and B.M.C., unpublished data). Virtually none of the roads we encountered had overhead canopy connections that would permit road-crossing movements by strictly arboreal species. Moreover, the inhibitory effects of roads on movements of larger animals will surely increase both as human activity and local hunting pressure rise (Peres 2000; Fa et al. 2005) and as road width increases. Across Gabon, roads appear to have negative, large-scale impacts on the abundance of forest elephants (Barnes et al. 1991; Lahm 1996), putty-nosed monkeys (Lahm et al. 1998), duikers and other antelope (Lahm 1991*b*), and other mammal species (Lahm 1992, 1993*b*; Lahm & Tezi 2006). Even in our sparsely populated study area, roads had a strong negative impact on the local abundance and distribution of duikers and forest elephants (Fig. 4).

National versus Multinational Corporations

Our study raises issues of both local and general relevance. Although the Rabi concession is being intensively managed for oil production, the prohibitions on hunting and nighttime driving, restricted access for nonemployees, and guidelines designed to minimize deforestation inside the oil concession are clearly having important benefits for wildlife. We encountered only very limited evidence of hunting inside the concession (a few snares and one abandoned hunting camp) and then only at one study site (R1) that was closest to the concession boundary (Fig. 1). Moreover, among all of our study sites outside the concession, the one nearest the concession (O2) had the highest mammal abundances, suggesting that Rabi concession might be acting as a population source and outside areas as a population sink for wildlife (e.g., Lahm 1993*b*; Novaro et al. 2000).

Hence, the Rabi oil concession is probably better protected from poaching and illegal encroachment than are most national parks in Gabon (e.g., Lahm 2001; Thibault & Blaney 2001; Alonso et al. 2006; Laurance et al. 2006) as a result of Shell-Gabon's environmental initiatives and measures to protect their valuable infrastructure and employees from accidents, theft, or terrorism. As a multinational conglomerate, Shell-Gabon's interests in environmental management at Rabi (including partial sponsorship of our research in the area) largely reflect their sensitivity to international opinion and pressures from consumers. In our experience in Africa and Latin America, smaller corporations based in developing nations are sometimes less interested and often less capable of financially investing in environmental protection. For example, Royal Dutch Shell, an international corporation, has recently agreed under pressure from environmental groups to reroute a controversial oil pipeline off Russia's east coast to reduce disturbances to the critically endangered western gray whale (*Eschrichtius robustus*) (Anonymous 2005). This contrasts starkly with the failed efforts of many scientists to convince Petrobras, a large Brazilian corporation, to forego a major road and oil-drilling operation in the heart of Yasuní National Park, the most important biological reserve in Ecuadorian Amazonia (e.g., ATBC 2005). The Petrobras road was only halted at the park border at the insistence of the Ecuadorian government.

This difference highlights a Faustian bargain that may become increasingly common in the tropics. As conservationists, do we pressure large, multinational corporations based in industrial nations to forego major projects in developing countries in an effort to limit environmental degradation, or do we favor such firms over smaller, national companies in the hope that they will be more sensitive to international pressures?

Future of the Rabi Corridor

Given its stable social conditions and substantially intact forest cover, Gabon is likely to play a crucial role in forest-conservation initiatives in central Africa (Kamdem-Toham et al. 2003; Laurance et al. 2006). Within Gabon, the general vicinity of the Rabi oil concession is very important from a regional perspective because it forms a biogeographic link between Loango and Moukalaba-Doudou national parks (Fig. 1). The Rabi corridor is thought to facilitate seasonal movements of forest elephants and other large wildlife species between inland and nearby coastal areas within the two parks (Alonso et al. 2006).

In this regional context, the future management of the Rabi area could be extremely important. At present, farming plots and villages are proliferating along oil and logging roads to the north of the Rabi oil concession, rapidly increasing local hunting pressure. A recent survey for poachers in the Gamba oil concession, a more densely populated area 60 km south of Rabi, reveals just how intensive hunting pressure can become. In only 3 days, a small field team found four hunting camps, three armed hunters, 149 snare traps (some containing live or dead wildlife and many targeting forest buffalo, a protected species), 18 spent shotgun shells, nine batteries for nighttime hunting with spotlights, and severe bark stripping of trees. Most snares and bark stripping occurred within a few meters of roads (Mbina et al. 2005; M.E.L., unpublished data).

Concerns about the future of Rabi are especially relevant because oil production in the concession has fallen sharply in the last decade and because Shell-Gabon is expected to eventually abandon its operation there. If and when this occurs, Rabi could experience a dramatic increase in hunting, logging, and slash-and-burn farming, as well as continued oil production by smaller companies. Instead of functioning as a protected-area buffer zone and likely faunal corridor between two important national parks, the broader Rabi area could instead become a major population sink for wildlife (e.g., Novarro et al. 2000; Peres 2001; Lahm & Tezi 2006). This would intensify deleterious edge effects and the demographic and genetic isolation of the parks, increasing the likelihood of local extinctions of vulnerable species (Woodroffe & Ginsberg 1998; Laurance et al. 2002).

Every effort should be made to forestall further degradation of the greater Rabi area. One option would be to grant the Rabi area sanctuary status under Gabonese law and to manage it under the auspices of an integrated conservation plan that includes its two adjoining parks (Loango and Moukalaba-Doudou) and nearby Mayumba National Park, which contains critical sea turtle nesting beaches. Such a plan might be achieved by designating the entire area as a biosphere reserve, which would allow planned development while affording high protection for core conservation areas (e.g., Kaus 1993). With effective long-term management, this region of southwestern Gabon could remain one of the most important areas for wildlife in Central Africa.

Acknowledgments

We thank R. Barnes, R. Didham, and two anonymous referees for commenting on the manuscript; CENAREST and Direction de la Faune et de la Chasse for research and entrance permits; and the Frank Bertrum Sherry Fund, Shell Foundation, Shell-Gabon, and Smithsonian Institution for financial and logistical support. This is contribution 44 of the Gabon Biodiversity Program.

Literature Cited

Alonso, A., M. Lee, P. Campbell, O. S. G. Pauwels, and F. Dallmeier, editors. 2006. Gamba, Gabon: biodiversity of an equatorial African rain forest. Bulletin of the Biological Society of Washington **12:**1–448.

Anon. 2005. Oil vs whales. New Scientist **186(2494)**:11.

ATBC (Association for Tropical Biology and Conservation). 2005. Resolution regarding road construction within Yasuní National Park and Biosphere Reserve, Ecuador. Society resolution. Association for Tropical Biology and Conservation, Washington, D.C. Available from www.atbio.org (accessed January 2005).

Barnes, R. F. W., K. L. Barnes, M. Alers, and A. Blom. 1991. Man determines the distribution of elephants in the rain forests of northeastern Gabon. African Journal of Ecology **29:**54–63.

Barnes, R. F. W., K. Beardsley, F. Michelmore, K. L. Barnes, M. Alers, and A. Blom. 1997. Estimating forest elephant numbers with dung counts and a geographic information system. Journal of Wildlife Management **61:**1384–1393.

Berre, A. D. 1998. Forests: Gabon's rich but untapped treasure. Leaders **21:**109–110.

CIA (Central Intelligence Agency). 2004. The world factbook: Gabon. CIA, Washington, D.C. Available from http://www.cia.gov/cia/publications/factbook/geos/gb.html (accessed July 2004).

Collomb, J. G., et al. 2000. A first look at logging in Gabon. Global Forest Watch, World Resources Institute, Washington, D.C.

Croes, B. M., W. F. Laurance, S. A. Lahm, L. Tchignoumba, A. Alonso, M. Lee, P. Campbell, and R. Buij. 2006. The influence of hunting on anti-predator behavior in central African monkeys and duikers. Biotropica **38:**in press.

De Bie, S., and C. Geerling. 1989. Ecological baseline study for oilfield development at Rabi, Gabon. Agricultural University, Wageningen, The Netherlands.

Develey, P., and P. C. Stouffer. 2001. Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. Conservation Biology **15:**1416–1422.

Fa, J. E., C. A. Peres, and J. Meeuwig. 2002. Bushmeat exploitation in tropical forests: an intercontinental comparison. Conservation Biology **16:**232–237.

Fa, J. E., S. F. Ryan, and D. J. Bell. 2005. Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afrotropical forests. Biological Conservation **121:**167–176.

Goosem, M. 1997. Internal fragmentation: the effects of roads, highways and powerline clearings on movement and mortality of rainforest vertebrates. Pages 241–255 in W. F. Laurance and R. O. Bierregaard Jr., editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago.

Johns, A. D. 1992. Vertebrate responses to selective logging: implications for the design of logging systems. Philosophical Transactions of the Royal Society, London B **335:**437–442.

Kamdem-Toham, A., A. W. Adeleke, N. Burgess, R. Carroll, J. D'Amico, E. Dinerstein, D. Olson, and L. Some. 2003. Forest conservation in the Congo Basin. Science **299:**346.

Kaus, A. 1993. Environmental perceptions and social relations in the Mapimí Biosphere Reserve. Conservation Biology **7:**398–406.

Koster, S. H., and J. A. Hart. 1988. Methods for estimating ungulate populations in tropical forests. African Journal of Ecology **26:**117–126.

Lahm, S. A. 1991a. Report on baseline study: mammal populations and human presence at Kango #1 drilling site, Abanga block. British Gas Gabon, Libreville.

Lahm, S. A. 1991b. Impact of human activity on antelope populations in Gabon. Gnusletter (IUCN Antelope Specialists Group) **10(1)**:7–8.

Lahm, S. A. 1992. Report on baseline study: mammal populations and human presence at Remboué III drilling site, Abanga block. British Gas Gabon, Libreville.

Lahm, S. A. 1993a. Utilization of forest resources and local variations of wildlife populations in northeastern Gabon. Pages 213—227 in C. M. Hladik, A. Hladik, O. F. Linares, H. Pagezy, A. Semple, and M. Hadley, editors. Tropical forests, people and food: biocultural interactions and applications to development. UNESCO, Paris.

Lahm, S. A. 1993b. Ecology and economics of human/wildlife interaction in northeastern Gabon. Ph.D. dissertation. New York University, New York.

Lahm, S. A. 1994. Impact of elephants on agriculture-Gabon. African Elephant Conservation Programme. Final report. Volume 4. European Commission, Ecology in Developing Countries Programme, Oxford, United Kingdom.

Lahm, S. A. 2001. Hunting and wildlife in northeastern Gabon: why conservation should extend beyond park boundaries. Pages 344–354 in W. Weber, L. J. T. White, A. Vedder, and N. Naughton-Treves, editors. African rain forest ecology and conservation. Yale University Press, New Haven, Connecticut.

Lahm, S. A., R. F. Barnes, K. Beardsley, and P. Cervinka. 1998. A method for censusing the greater white-nosed monkey in northeastern Gabon using the population density gradient in relation to roads. Journal of Tropical Ecology **14:**629–643.

Lahm, S. A., and J. P. Tezi. 2006. Assessment of the communities of medium-sized and large arboreal and terrestrial mammals in the Rabi-Toucan region of the Ngové-Ndogo Hunting Domain and southwestern Loango National Park. Bulletin of the Biological Society of Washington **12:**383–416.

Laurance, S. G. W., P. C. Stouffer, and W. F. Laurance. 2004. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. Conservation Biology **18:**1099–1109.

Laurance, W. F. 2001. Tropical logging and human invasions. Conservation Biology **15:**4–5.

Laurance, W. F., A. Alonso, M. Lee, and P. Campbell. 2006. Challenges for forest conservation in Gabon, central Africa. Futures **38:**454–470.

Laurance, W. F., T. Lovejoy, H. Vasconcelos, E. Bruna, R. Didham, P. Stouffer, C. Gascon, R. Bierregaard, S. Laurance, and E. Sampiao. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation Biology **16:**605–618.

Laurance, W. F., and C. A. Peres, editors. 2006. Emerging threats to tropical forests. University of Chicago Press, Chicago.

Malcolm, J. R., and J. C. Ray. 2000. Influence of timber extraction routes on central African small-mammal communities, forest structure, and tree diversity. Conservation Biology **14:**1623–1638.

Mbina, A. M., O. S. G. Pauwels, M. Onanga, E. Tobi, S. Mboumba. 2005. Rapporte de patrouille Totou 9: routes de production Shell-Gabon. Direction de la Fauna et de la Chasse, Parc National Loango-sud, Gamba, Gabon.

McCune, B., and M. J. Mefford. 1999. PC-ORD: multivariate analysis of ecological data, Version 4.17. MjM Software, Glenenden Beach, Oregon.

Milner-Gulland, E. J., E. L. Bennett, and the SCB 2002 Annual Meeting Wild Meat Group. 2003. Wild meat: the bigger picture. Trends in Ecology & Evolution **18:**351–357.

Mason, D. J., and J.-M. Thiollay. 2001. Tropical forestry and the conservation of neotropical birds. Pages 167–191 in R. A. Fimbel, A. Grajal, and J. G. Robinson, editors. The cutting edge: conserving wildlife in logged tropical forests. Columbia University Press, New York.

Naughton-Treves, N., and W. Weber. 2001. Human dimensions of the African rain forest. Pages 20–46 in W. Weber, L. J. T. White, A. Vedder, and N. Naughton-Treves, editors. African rain forest ecology and conservation. Yale University Press, New Haven, Connecticut.

Noss, A. J. 1998. The impacts of cable snare hunting on wildlife populations in the forests of the Central African Republic. Conservation Biology **12:**390–398.

Novaro, A. J., K. H. Redford, and R. E. Bodmer. 2000. Effect of hunting in source-sink systems in the Neotropics. Conservation Biology **14:**713–721.

Oates, J. F., M. Abedi-Lartey, W. McGraw, T. T. Struhsaker, and G. Whitesides. 2000. Extinction of a West African red colobus monkey. Conservation Biology **14:**1526–1532.

Olson, D. M., and E. Dinerstein. 1998. The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. Conservation Biology **12:**502–515.

Peres, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. Conservation Biology **14:**240–253.

Peres, C. A. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. Conservation Biology **15:**1490–1505.

Robinson, J. G., K. H. Redford, and E. L. Bennett. 1999. Wildlife harvest in logged tropical forests. Science **284:**595–596.

Roldán, A. and J. A. Simonetti. 2001. Plant-mammal interactions in tropical Bolivian forests with different hunting pressures. Conservation Biology **15:**617–623.

Soriano, P. J., and J. Ochoa G. 2001. The consequences of timber exploitation for bat communities in tropical America. Pages 153–166 in R. A. Fimbel, A. Grajal, and J. G. Robinson, editors. The cutting edge: conserving wildlife in logged tropical forests. Columbia University Press, New York.

Thibault, M., and S. Blaney. 2001. Sustainable human resources in a protected area in southwestern Gabon. Conservation Biology **15:**591–595.

Trebaol, L., and C. Chaillol. 2002. Environmental and social impacts of oil industry activities in central Africa: a case study on the Gamba Protected Areas Complex (Gabon). World Wide Fund for Nature, Gamba, Gabon.

Tutin, C. E. G., and M. Fernandez. 1984. Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. American Journal of Primatology **6:**313–336.

White, L. J. T., and C. E. G. Tutin. 2001. Why chimpanzees and gorillas respond differently to logging: a cautionary tale from Gabon. Pages 449–462 in W. Weber, L. J. T. White, A. Vedder, and N. Naughton-Treves, editors. African rain forest ecology and conservation. Yale University Press, New Haven, Connecticut.

Whitesides, G. H., J. F. Oates, S. M. Green, and R. P. Kluberdanz. 1988. Estimating primate densities from transects in a West African rain forest: a comparison of techniques. Journal of Animal Ecology **57:**345–367.

Wilkie, D. S., and J. F. Carpenter. 1999. Bushmeat hunting in the Congo Basin: an assessment of impacts and options for management. Biodiversity and Conservation **8:**927–955.

Wilkie, D. S., and N. Laporte. 2001. Forest area and deforestation in central Africa: current knowledge and future directions. Pages 119–139 in W. Weber, L. J. T. White, A. Vedder, and N. Naughton-Treves, editors. African rain forest ecology and conservation. Yale University Press, New Haven, Connecticut.

Wilkie, D. S., E. Shaw, F. Rothberg, G. Morelli, and P. Auzel. 2000. Roads, development, and conservation in the Congo Basin. Conservation Biology **14:**1614–1622.

Wilkie, D. S., J. G. Sidle, and G. C. Boundzanga. 1992. Mechanized logging, market hunting, and a bank loan in Congo. Conservation Biology **6:**570–580.

Wilkie, D. S., M. Starkey, K. Abernathy, E. N. Effa, P. Telfer, and R. Godoy. 2005. Role of prices and wealth in consumer demand for bushmeat in Gabon, central Africa. Conservation Biology **19:**268–274.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science **280:**2126–2128.

Wright, S. J. 2003. The myriad consequences of hunting for vertebrates and plants in tropical forests. Perspectives in Plant Ecology, Evolution and Systematics **6:**73–86.