

# Impacts of Roads, Hunting, and Habitat Alteration on Nocturnal Mammals in African Rainforests

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**Abstract:** Nocturnal mammals are poorly studied in Central Africa, a region experiencing dramatic increases in logging, roads, and hunting activity. In the rainforests of southern Gabon, we used spotlighting surveys to estimate abundances of nocturnal mammal species and guilds at varying distances from forest roads and between hunted and unhunted treatments (comparing a 130-km<sup>2</sup> oil concession that was nearly free of 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 along road verges and at 50, 300, and 600 m from the road. We then repeatedly surveyed mammals at each site during 2006. Hunting had few apparent effects on this assemblage. Nevertheless, the species richness and often the abundance of nocturnal primates, smaller ungulates, and carnivores were significantly depressed within approximately 30 m of roads. Scansorial rodents increased in abundance in hunted forests, possibly in response to habitat changes caused by logging or nearby swidden farming. In multiple-regression models many species and guilds were significantly influenced by forest-canopy and understory cover, both of which are altered by logging and by certain abiotic variables. In general, nocturnal species, many of which are arboreal or relatively small in size (<10 kg), were less strongly influenced by hunting and more strongly affected by human-induced changes in forest structure than were larger mammal species in our study area.

**Keywords:** African rainforest, bushmeat, Gabon, hunting, logging, nocturnal mammals, oil development, road effects

Impactos de Carreteras, Cacería y Alteración del Hábitat sobre Mamíferos Nocturnos de Bosques Lluviosos Africanos

**Resumen:** Los mamíferos nocturnos casi no han sido estudiados en África Central, una región que experimenta un incremento dramático de tala, carreteras y actividades cinegéticas. En los bosques lluviosos del sur de Gabón, utilizamos muestreos con lámparas para estimar las abundancias de especies y gremios de mamíferos nocturnos a distintas distancias de carreteras y entre tratamientos con y sin cacería (comparamos una concesión petrolera de 130 km<sup>2</sup> que prácticamente estaba libre de cacería con áreas afuera de la concesión que tenían presión cinegética moderada). Establecimos transectos de 1 km a lo largo de carreteras y a 50 m, 300 m y 600 m de la carretera en cada uno de los 12 sitios de estudio, que estaban divididos en áreas con y sin cacería. Posteriormente, muestreamos mamíferos en cada sitio durante 2006. La cacería tuvo pocos efectos aparentes sobre este ensamble. Sin embargo, la riqueza de especies y, a menudo, la abundancia de los primates nocturnos, de ungulados pequeños y de carnívoros disminuía significativamente a ~30 m de las carreteras. La abundancia de roedores trepadores incrementó en los bosques con cacería, posiblemente como respuesta a los cambios de hábitat provocados por la tala o la agricultura de tumba-roza-quema. En los modelos de regresión múltiple, muchas especies y gremios fueron influidos significativamente por la cobertura del dosel y del sotobosque, que son alteradas por la tala y ciertas variables abióticas. En general, las especies nocturnas, muchas de las cuales son arborícolas o de tamaño relativamente pequeño (<10 kg),

*fueron menos afectadas por la cacería, pero más afectadas por los cambios en la estructura del bosque inducidos por humanos, que las especies de mamíferos mayores en nuestra área de estudio.*

**Palabras Clave:** bosque lluvioso Africano, cacería, carne de monte, desarrollo petrolero, efectos de carreteras, Gabón, mamíferos nocturnos, tala

## Introduction

The rainforests of Central Africa are a key global conservation priority because of their high biological uniqueness and rapid rates of loss and degradation (Olson & Dinerstein 1998; Fonseca et al. 2000; Kamdem-Toham et al. 2003). Nearly half of all Central-African forests have been destroyed (Naughton-Treves & Weber 2001), and much of the remainder are threatened by industrial logging, slash-and-burn farming, road and infrastructure projects, and overhunting (Lahm et al. 1998; Laurance et al. 2006a; Blake et al. 2007; Laporte et al. 2007).

Perhaps the most immediate threat to wildlife in Central Africa is the alarming synergism between logging and hunting (Barnes et al. 1997; Fa et al. 2005; Laurance & Peres 2006). Logging has grown dramatically in countries such as Cameroon (Ndoye & Kaimowitz 2000), the Republic of Congo (Elkan et al. 2006; Laporte et al. 2007), and Gabon (Collomb et al. 2000; Laurance et al. 2006a) and could soon expand by up to 60-fold in the vast Democratic Republic of Congo (Rainforest Foundation 2004). By creating networks of forest roads, logging allows hunters to reach unexploited wildlife populations (Robinson et al. 1999; Wilkie et al. 2000; Blake et al. 2007) and lowers the cost of transporting bushmeat to market (Wilkie et al. 1992). The efficiency of hunters has also increased as shotguns and cable snares have replaced traditional crossbows, spears, and nets (Lahm 1993; Noss 1998). These striking changes in forest access and hunting efficiency, in concert with continuing human-population growth, are driving a burgeoning commercial bushmeat trade (Milner-Gulland et al. 2003) that is making Central Africa one of the most intensively hunted tropical regions in the world (Wilkie & Carpenter 1999; Fa et al. 2002; van Vliet et al. 2007). Of 57 mammal, bird, and reptile species hunted in the region, 60% are currently being exploited unsustainably (Fa et al. 2005; see also Robinson & Bennett 2004).

Clearly, there is a dire need to better understand the impacts of roads and hunting on Central African wildlife. In a biologically important area of southwestern Gabon (Alonso et al. 2006), we recently assessed the effects of roads and hunting on a diverse mammal assemblage, using daytime surveys of mammals and their signs along a series of forest transects. Our findings indicate that even moderate hunting pressure has far-reaching impacts on the abundance, guild composition, and behavior of many ungulate, primate, and carnivore species, and that

road avoidance by larger mammals increases as hunting pressure intensifies (Laurance et al. 2006b; Croes et al. 2007).

We extended this work by evaluating the impacts of roads, hunting, and human-induced habitat alteration on nocturnal mammals. Our study was important in several respects. First, many nocturnal species in African rainforests have been little studied (e.g., Lahm 1993) and their responses to hunting and land-use change are not well understood. Spotlighting is an effective technique for censusing nocturnal wildlife (Laurance 1990, 1991) and is the only feasible way to assess the abundance of many arboreal species, such as galagos, pottos, arboreal rodents, tree pangolins, certain civets and genets, and tree hyraxes, that are not detectable with daytime surveys. (Table 1 lists the scientific names of these species.) Second, we carefully designed and replicated our surveys and included an experimental control area (a large oil concession) that was almost entirely protected from hunting. This design allowed us to rigorously assess the relative effects of roads, hunting, and habitat alteration on different nocturnal species and guilds. Finally, our results have general and key local relevance because our study area is a potentially critical corridor between 2 recently designated national parks in Gabon and its future is far from secure.

## Methods

### Study Area

Our study area (Fig. 1) in southwestern Gabon (1° 55'S, 9° 50'E) encompassed approximately 400 km<sup>2</sup>, of which 130 km<sup>2</sup> was the Rabi oil concession, the highest-producing onshore oilfield in sub-Saharan Africa, operated by Shell-Gabon Corporation since 1985 (Trebaol & Chaillol 2002). The study area is part of an important forest corridor between 2 recently established national parks, Loango (1550 km<sup>2</sup>) to the west and Moukalaba-Doudou (4500 km<sup>2</sup>) to the east (Alonso et al. 2006).

The region is dominated by old-growth and selectively logged, lowland tropical rainforest. Annual rainfall averages approximately 2300 mm and is highly seasonal, with dry seasons from June to October and mid-December to mid-January. The terrain is undulating, with rainforest on hills and slopes and seasonally inundated forest or swamps in gullies (de Bie & Geerling 1989). Further

**Table 1. Pearson correlations of nocturnal mammal species surveyed in Gabon with 3 ordination axes.<sup>a</sup>**

Common name	Scientific name	Axis 1	Axis 2	Axis 3
<b>Arboreal species</b>				
Demidoff's galago <sup>b</sup>	<i>Galago demidoff</i>	−0.616*	0.433*	−0.553*
Allen's squirrel galago	<i>G. alleni</i>	−0.545*	−0.619*	0.241
elegant needle-clawed galago	<i>Euoticus elegantulus</i>	0.419*	0.205	0.786*
potto	<i>Perodicticus potto</i>	−0.222	0.311	0.052
Beecroft's anomalure	<i>Anomalurus beecrofti</i>	0.014	−0.219	−0.093
Lord Derby's anomalure	<i>A. derbianus</i>	0.362	0.341	0.117
lesser anomalure	<i>A. pusillus</i>	0.231	−0.087	0.156
Cameroon scaly-tail	<i>Zenkerella insignis</i>	0.428*	0.137	0.614*
African palm civet	<i>Nandinia binotata</i>	0.506*	0.021	0.138
servaline genet	<i>Genetta servalina</i>	−0.243	−0.047	0.039
tree pangolin	<i>Phataginus tricuspis</i>	0.330	0.531*	0.448*
tree hyrax	<i>Dendrohyrax dorsalis</i>	0.133	−0.182	0.037
<b>Terrestrial and scansorial species</b>				
brush-tailed porcupine	<i>Atherurus africanus centralis</i>	−0.325	−0.085	0.144
murid rodents <sup>c</sup>	<i>Muridae</i>	−0.131	−0.049	−0.095
African forest elephant	<i>Loxondonta africana cyclotis</i>	−0.330	0.244	−0.136
water chevrotain	<i>Hyemoschus aquaticus</i>	−0.213	0.072	0.022
blue duiker	<i>Cephalophus monticola defriesi</i>	−0.405	−0.710*	−0.282
Ogilby's duiker	<i>C. ogilbyi crusalbaum</i>	−0.170	−0.243	0.072
yellow-backed duiker	<i>C. silvicultor</i>	0.105	0.030	−0.199
bay duiker	<i>C. dorsalis castaneus</i>	0.098	−0.254	−0.065
Peter's duiker	<i>C. callipygus callipygus</i>	−0.115	−0.341	0.080
Variation explained (%) <sup>d</sup>		40.2	29.8	22.1

<sup>a</sup>An asterisk indicates significance at the  $p = 0.003$  level, which was determined with a Bonferroni correction to reduce the likelihood of spurious correlations.

<sup>b</sup>These could include Thomas' galagos (*Galago thomasi*), which are difficult to distinguish visually from Demidoff's galagos.

<sup>c</sup>Small (10–150 g) mice and rats, predominantly in the family Muridae.

<sup>d</sup>Coefficient of determination for the correlation between ordination distances and distances in the original  $n$ -dimensional space.

details on the study area are provided by Laurance et al. (2006b).

Access to Rabi is strictly regulated by Shell-Gabon, which maintains guard posts at all road-access points. Although several hundred oilfield workers are stationed at Rabi, hunting and possession of firearms, snares, and bushmeat are stringently forbidden, and employees are not allowed to leave their camps after nightfall. Efforts have also been made to minimize deforestation, replant some deforested areas, and regulate roadwork. Despite a network of unpaved roads and clearings for wellheads, field camps, and infrastructure, approximately 90% of the original forest cover has been maintained inside the Rabi concession.

Outside the concession, selective logging and oil operations are ongoing in several areas, and forest damage is generally heavier and more recent. Although the density of permanent roads is lower than inside the concession (Fig. 1), roads tend to be wider. The human population within a 20-km radius of Rabi is sparse, averaging <1 resident/km<sup>2</sup> (Trebaol & Chaillol 2002) in scattered villages and logging camps that range from a few to a few dozen families. Mosaics of farming plots and regrowth often occur within 1–2 km of villages. The expansion of roads from oil and logging activities is facilitating some commercial hunting, with bushmeat being sold openly in

regional towns such as Gamba and Tchibanga (Trebaol & Chaillol 2002).

### Sampling Design

We used a stratified random design to select 12 study sites (Fig. 1), half inside and half outside the Rabi oil concession (see Laurance et al. [2006b] for details). All sites had a relatively straight road and no other active roads or clearings nearby. Study sites outside the concession were all <5 km linear distance from a small village or logging camp, and were dominated by mature forest with little if any regrowth or farming plots. At each site we established 4 1-km-long, linear, parallel transects, 1 along the road and 3 others at 50, 300, and 600 m from the road margin. We cut narrow trails along each transect with machetes, marked the transect at 50-m intervals, and then waited  $\geq 10$  days before commencing spotlighting surveys. Compared with our earlier daytime study, 2 of our study sites (O3 and O6) were shifted 1–1.5 km southward and a third site (R1) was moved 200 m eastward to avoid inundated or particularly steep areas that would have been difficult to hike at night.

The 12 sites (48 transects) were surveyed 4 times each in 2006, from the early dry season to early wet season (late May to early October), with a minimum 2-week interval between successive surveys of any site. Surveys were

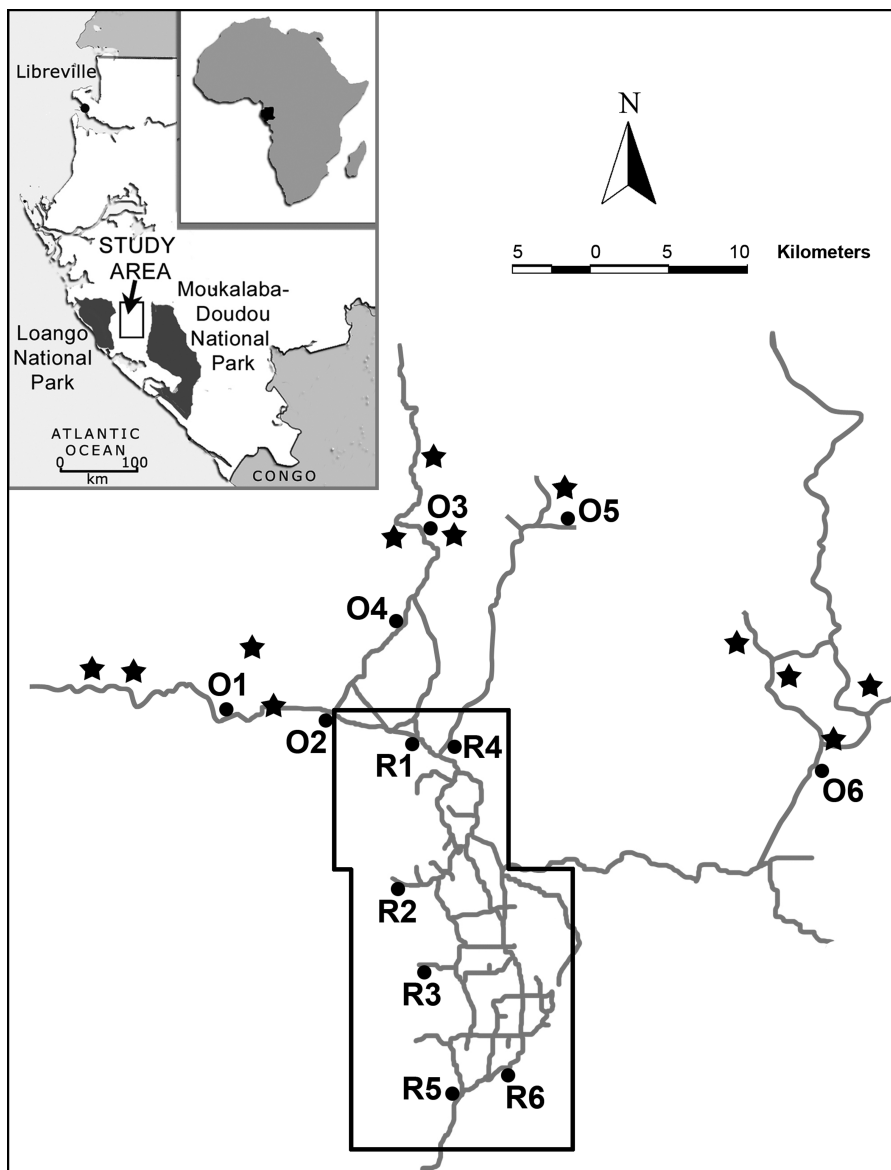


Figure 1. Map of the study area in southwestern Gabon, showing locations of study sites within the Rabi oil concession (sites R1–R6), where hunting is prohibited, and outside the concession (sites O1–O6), where hunting pressure is generally moderate. Wavy gray lines indicate roads, stars show locations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

conducted by spotlighting at night with an experienced 3-person team, 2 members of which were Gabonese field technicians with prior hunting experience. Headlamps and 30-W spotlights were used to detect animals and their eyeshines. The team hiked slowly (0.5–1 km/h) and quietly through the forest, stopping every 4–6 m to scan in all directions. Species were usually identified with binoculars, but a few common galago and anomalure species were also identified from their distinctive barks or calls (such identifications were recorded only for individuals judged to be <50 m from the transect line).

All spotlighting surveys were conducted between 20:00 and 04:00. Two nights were required to survey each site, with the transects at 50 and 600 m from the road surveyed on 1 night and transects 300 m from the road and along the road itself surveyed on a different night. To minimize any effects of time of night on animal activity, we alternated the sequence in which each

transect-pair was surveyed (e.g., initially surveying the 50-m transect and then the 600-m transect, and then reversing this for the following survey). We also alternated the direction that we hiked each transect (e.g., initially moving north to south and then south to north). Finally, to minimize any effects of seasonality or weather variability on our results, we alternated the surveys between sites inside versus outside of Rabi oil concession, with the initial sequence of sites chosen randomly.

The duration of each transect survey was recorded in minutes. We derived a standardized abundance estimate for each species (number of individuals per hour) for each transect by pooling data across all surveys and then dividing the total number of individuals detected by the total number of hours spent surveying the transect. For each animal we also estimated its lateral distance from the transect line or road edge; its height (for arboreal species); the total number of individuals, if accompanied

by conspecifics; and any notable observations of animal behavior or age.

### Hunting and Habitat Data

Along each of the 36 forest transects, we recorded an index of hunting pressure for each 50-m segment based on signs of human activity: 1, old trail or abandoned hunting camp; 2, old snare trap or gun shell; 3, fresh trail or active snare trap; 4, gunshot heard. These data were collected continuously throughout the study and then summed to form a single composite value for each transect. In addition, for every 50-m segment we collected data on 6 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 cover (1, low; 2, moderate; 3, high); (3) canopy cover (1, <50%; 2, 50–75%; 3, >75% cover); (4) logging damage, determined on the basis of old logging tracks or cut stumps (1, none; 2, light; 3, heavy or recent); (5) topographic position (1, gully bottom; 2, lower slope; 3, upper slope; 4, ridgetop/plateau); and (6) slope (0, flat; 1, 1–25% grade; 2, 25–50% grade; 3, >50% grade). Habitat data were averaged for each transect.

We recorded only a single environmental variable, road-clearing width, for the 12 road transects, which differed fundamentally in vegetation structure from the 36 forest transects. The width of each road clearing (including margins) was determined with a tape measure at 100-m intervals (11 measurements/site).

### Data Analysis

We quantified mammal assemblages in 3 ways. First, species-level analyses were conducted for the most abundant species. Second, species were pooled into 5 functional guilds: (1) nocturnal primates (galagos and potto), (2) gliding rodents (anomalures and Cameroon scaly-tail), (3) scansorial rodents (brushtailed porcupine, giant pouched rat, murids), (4) smaller ungulates (duikers and water chevrotain), and (5) carnivores (leopard [*Panthera pardus pardus*], African civet [*Civettictis civetta*], palm civet, servaline genet, Central African linsang [*Potiana richardsoni*], marsh mongoose [*Atilax paludinosus*]). Species within the same guild were assumed to have similar detectability, despite differences in behavior or body size. A few ecologically unique or rarely encountered species (tree pangolin [*Phataginus tricuspis*], tree hyrax, forest elephant, red river hog [*Potamochoerus porcus*]) were not assigned to guilds. Third, nonmetric multidimensional scaling (NMS), 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  $\log(x + 1)$ -transformed data on species abundances, excluding rare species (detected at <4 transects), with Sorensen's distance metric. Randomization tests ( $n = 250$ ) were used to determine the

number of ordination axes that explained significantly more variation than expected by chance.

For the mammal guilds and relatively abundant species (detected at  $\geq 5$  transects), we used 2-way analyses of variance (ANOVAs) to test effects of the hunting "treatment" (inside vs. outside the Rabi concession) and the 4 road-distance categories (road margins and 50, 300, and 600 m from the road). For the 36 forest transects, best-subsets and multiple regressions were also used to identify combinations of environmental variables (hunting pressure, logging, canopy cover, understory cover, topographic position, slope, soil inundation) that influenced mammal abundance. We excluded road transects from this analysis because conditions along roads were fundamentally different from those on forest transects and would have been strong outliers. Mammal abundance data were  $\log(x + 1)$  transformed as needed to reduce heteroscedasticity and improve normality.

## Results

### Hunting and Habitat Variables

Among the 36 forest transects, 83% of those outside Rabi oil concession had signs of nearby hunting activity, versus just 11% of those inside the concession. Evidence of hunting pressure was significantly higher outside than inside the concession ( $F_{1,30} = 103.4$ ,  $p < 0.00001$ ) but did not vary significantly as a function of distance to roads ( $F_{2,30} = 1.53$ ,  $p = 0.23$ ; 2-way ANOVA). Across the 12 study sites, the average hunting-pressure index (mean score for all forest transects) was strongly and negatively correlated with linear distance to the nearest village or logging camp ( $r_s = -0.912$ ,  $p = 0.00004$ ; 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 m [8.6]) than inside (18.8 m [4.0]) the concession ( $t = 2.29$ ,  $df = 10$ ,  $p = 0.045$ ;  $t$  test with log-transformed data). In addition, forest transects outside the concession had significantly heavier logging ( $F_{1,30} = 10.95$ ,  $p = 0.002$ ), reduced canopy cover ( $F_{1,30} = 4.54$ ,  $p = 0.041$ ), and heavier understory cover ( $F_{1,30} = 6.96$ ,  $p = 0.013$ ; 2-way ANOVAs). In fact, logging intensity was a highly significant predictor of canopy cover (slope negative;  $F_{1,34} = 40.29$ ,  $R^2 = 54.2\%$ ,  $p < 0.00001$ ) and understory cover (slope positive;  $F_{1,34} = 7.79$ ,  $R^2 = 18.6\%$ ,  $p = 0.009$ ; linear regressions). Among the forest transects, distance to the road had few significant effects on environmental variables. Transects 600 m from the road had lower topographic positions ( $p < 0.05$ ) and more soil inundation ( $p < 0.001$ ) than did those 50 m from the road (Tukey's tests), but no other variables differed significantly ( $p > 0.10$ ; 2-way ANOVAs).

### Forest Structure and Animal Detectability

Overall, we detected 1403 individuals of 27 mammal species (not including murid rodents, which were small in size [ $<150$  g] and identified only at the family level). Spotlighting conditions were generally easier along roads than along forest transects because walking was less strenuous on road surfaces than over dense, undulating forest terrain and because one could move back several meters from the vegetation along roads and thereby gain better sight lines. Forest edges adjoining roads often had dense cover from proliferating vines and lateral-branch growth, but this was patchy and still allowed views of all vertical layers of the forest, including the ground layer. As a result of these structural differences, the mean horizontal distances that animals could be detected into the forest was significantly greater ( $F_{3,1395} = 7.12, p < 0.001$ ) along road margins (mean [SD] = 13.1 m [11.1]) than in forest-interior transects (9.9 m [7.2]), but did not differ significantly inside versus outside the Rabi oil concession ( $F_{1,1395} = 2.73, p = 0.098$ ; 2-way ANOVA with log-transformed data). Along roads, 95% of all animals were detected within 32 m of the road margin, whereas along the forest transects, 95% of animals were detected within 21 m of the transect line.

Logging did not evidently affect the distance to which animals could be detected into the forest. Among the 36 forest transects, there was no significant association between the logging index and the median horizontal distance to which animals could be detected into the forest ( $F_{1,34} = 0.05, R^2 = 0.2\%, p = 0.82$ ). Likewise, none of the other habitat variables significantly influenced the horizontal detection distance among the forest transects ( $p > 0.19$  in all cases; all linear regressions with log-transformed distance data).

### Ordination of Mammal Communities

The ordination analysis of data on 21 relatively abundant species (detected at  $\geq 4$  transects) revealed 3 major gradients in species composition, with the axes capturing 40.2%, 29.8%, and 22.1% of the total variation in the data set, respectively (Table 1). The first axis distinguished transects with many Demidoff's and Allen's squirrel galagos, from those with many palm civets, Cameroon scaly-tails, and elegant needle-clawed galagos. Axis 2 separated transects with many blue duikers and Allen's squirrel galagos, from those with many tree pangolins and Demidoff's galagos. Axis 3 distinguished transects with many Demidoff's galagos from those with many elegant needle-clawed galagos, Cameroon scaly-tails, and tree pangolins (Table 1).

No ordination axes differed significantly inside versus outside Rabi concession (Table 2), suggesting that hunting had relatively little impact on mammal community structure. Nevertheless, among transects at differing dis-

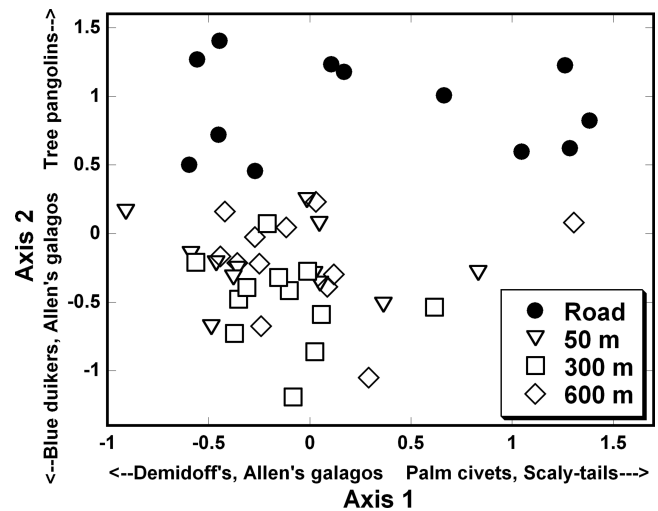


Figure 2. Plot of nocturnal-mammal assemblages in ordination space, contrasting surveys of forest margins with those at 50, 300, and 600 m from roads.

tances from forest roads, axis-2 scores were much higher on road margins than on forest transects ( $p < 0.001$ , Tukey's test), indicating that mammal assemblages near roads were distinct from those inside the forest (Fig. 2). Scores on axes 1 and 3 did not vary significantly with distance from roads (Table 2).

### Guilds and Species

The effects of hunting and road proximity on 5 mammal guilds were similar (Table 2). Only scansorial rodents differed significantly between hunted and unhunted sites, and their abundance actually increased in hunted forest. Proximity to roads, however, had much wider effects, leading to significantly increased abundances of nocturnal primates, reduced abundances of small ungulates, and significantly reduced species richness of nocturnal primates, carnivores, and small ungulates (Fig. 3). In all cases, the only significant differences were between road margins and transects inside the forest (Table 2).

Hunting and roads had similar effects on the 17 most frequently detected mammals (including murid rodents, pooled at the family level; Table 2). Three species—Allen's squirrel galago, blue duiker, and Ogilby's duiker—exhibited significant (or nearly significant) declines on road margins relative to forest transects, whereas a fourth species—tree pangolins—increased on road margins. The only taxa that differed significantly (or nearly significantly) between the hunted and unhunted sites were murid rodents and the brush-tailed porcupine, and both were more abundant in hunted sites. Hence, only scansorial rodents appeared to be affected by hunting and their response was actually positive, whereas a broader suite of species responded significantly to road proximity.

**Table 2.** Effects of hunting pressure (comparing inside vs. outside an unhunted oil concession) and proximity to roads (comparing road edges and forest transects 50, 300, and 600 m from roads) on nocturnal-mammal communities in Gabonese rainforests, with 2-way analysis of variance.<sup>a</sup>

Response variable	Hunting pressure		Road proximity		Tukey's tests (p)
	F <sub>1,40</sub>	p	F <sub>3,40</sub>	p	
Ordination axes					
axis 1	0.99	0.33	1.72	0.18	
axis 2	0.03	0.87	41.27	<0.0001	road > all forest transects (<0.001)
axis 3	0.08	0.78	0.13	0.94	
Abundances of mammal guilds					
nocturnal primates <sup>b</sup>	1.18	0.28	4.92	0.005	road > 300-m (<0.01) and 600-m (<0.05) transects
gliding rodents <sup>b</sup>	1.41	0.24	1.14	0.34	
scansorial rodents <sup>b</sup>	9.35	0.004	2.38	0.084	hunted > unhunted (<0.01)
carnivores	0.01	0.91	1.37	0.37	
small ungulates	0.18	0.67	9.94	0.0001	road < all forest transects (50 m, <0.001; 300 m, and 600 m, <0.01)
Species richness of mammal guilds					
nocturnal primates	0.82	0.37	9.53	0.0001	road < all forest transects (<0.001)
gliding rodents	2.25	0.14	0.05	0.99	
carnivores	0.07	0.79	2.97	0.043	road < 600-m transect (0.052)
small ungulates	0.42	0.52	10.21	<0.0001	road < all forest transects (50-m, <0.001; 300-m and 600-m, <0.01)
Abundances of more common species <sup>c</sup>					
Demidoff's galago <sup>b,d</sup>	1.89	0.18	2.04	0.12	
Allen's squirrel galago	1.83	0.18	10.78	<0.0001	road < all forest transects (<0.001)
Elegant needle-clawed galago <sup>b</sup>	0.18	0.67	0.35	0.79	
potto <sup>b</sup>	0.93	0.34	0.43	0.74	
Cameroon scaly-tail <sup>b</sup>	0.52	0.48	1.33	0.28	
Lord Derby's anomalure <sup>b</sup>	1.16	0.29	2.35	0.086	
brush-tailed porcupine <sup>b</sup>	3.26	0.079	2.44	0.078	
murid rodents <sup>b</sup>	5.62	0.023	0.51	0.68	hunted > unhunted (<0.03)
palm civet <sup>b</sup>	0.37	0.54	0.62	0.61	road > all forest transects (50-m and 300-m, <0.02; 600-m, <0.05)
tree pangolin	0	0.96	4.53	0.008	
tree hyrax <sup>b</sup>	0.11	0.74	1.27	0.3	
forest elephant	0.29	0.59	1.47	0.24	
blue duiker	0.1	0.76	7.1	0.0006	road < all forest transects (<0.01)
Ogilby's duiker <sup>b</sup>	0.12	0.73	2.29	0.093	road < 50 m (<0.08)
yellow-backed duiker <sup>b</sup>	0.08	0.78	0.29	0.83	
bay duiker	0.05	0.82	1.89	0.15	
Peter's duiker	0.38	0.54	2.71	0.058	

<sup>a</sup>Interaction effects are not shown because only one interaction was statistically significant (Peter's duiker,  $p = 0.005$ ).

<sup>b</sup>Data were  $\log(x + 1)$  transformed.

<sup>c</sup>Species detected on at least 5 transects.

<sup>d</sup>May include Thomas' galagos.

## Habitat Predictors

In our assessment of the effects of our 7 habitat predictors on mammal guilds and frequently detected species (Table 3), only logging and canopy cover were intercorrelated enough ( $R^2 = 54\%$ ) to create significant collinearity effects in the regression models. In no cases were both predictors selected for the same model.

Three trends were apparent (Table 3). First, hunting pressure was a significant predictor only for rodents, and in all cases the effects were positive. Both rodent guilds (gliding and scansorial rodents) increased in abundance

in hunted forest. Among the abundant rodent taxa, the Cameroon scaly-tail (a gliding rodent), brush-tailed porcupine, and murid rodents all responded positively to hunting. Second, more than half (7/13) of the frequently detected mammal species were either negatively associated with logging (potto) or were significantly influenced by forest-canopy or understory cover (Allen's squirrel galago, elegant needle-clawed galago, brush-tailed porcupine, palm civet, blue duiker, Peter's duiker), which can be strongly affected by logging. Third, edaphic variables (slope, topographic position, soil inundation) significantly affected nearly a third (4/13) of the frequently

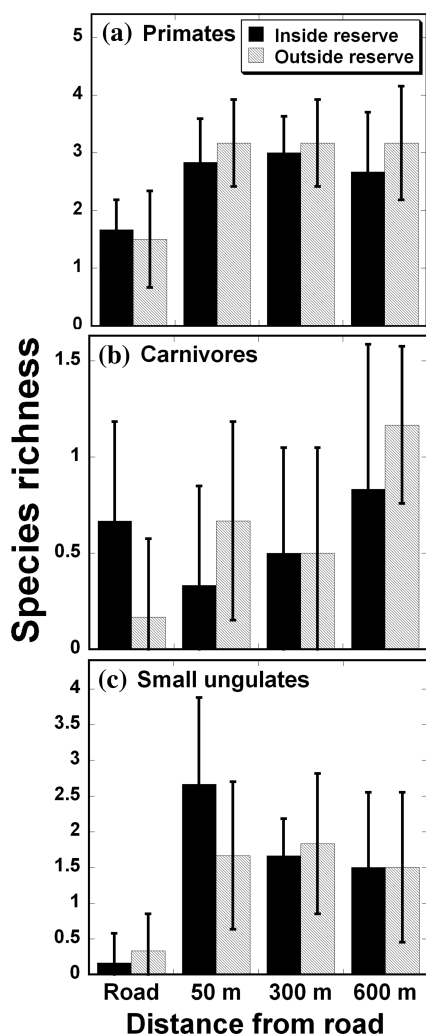


Figure 3. Species richness (mean [SD]) of (a) primates, (b) carnivores, and (c) small ungulates in hunted versus unhunted rainforests and as a function of distance from forest roads.

detected species, and influenced the abundance or species richness of 3 mammal guilds (nocturnal primates, gliding rodents, small ungulates). The relatively low coefficients of determination ( $R^2 < 20\%$ ) in several of the regression models (Table 3) likely occurred because habitat variables and mammal abundances were averaged over 1-km transects, obscuring finer-scale species-habitat relationships.

To evaluate the overall effects of our habitat predictors on mammal community structure, we conducted a second NMS ordination (with log-transformed abundances of the 15 most frequently detected mammal species along the 36 forest transects). A single ordination axis was selected, capturing 63.3% of the variation in the data set. This axis described a gradient between sites with many Demidoff's galagos, Allen's squirrel galagos, pottos, and Cameroon scaly-tails, and those with many palm civets ( $r > 0.329$ ,  $p < 0.05$  in all cases; Pearson correlations).

With best-subsets and multiple regressions, only a single predictor, canopy cover, was selected ( $F_{1,34} = 18.31$ ,  $R^2 = 35.0\%$ ,  $p = 0.0001$ ), and this was positively associated with the abundances of the galagos, pottos, and scaly-tails and negatively associated with palm civet abundance (Fig. 4a). Neither hunting pressure ( $F_{1,33} = 1.93$ ,  $p = 0.17$ ) nor distance to roads ( $F_{1,33} = 0.07$ ,  $p = 0.80$ ) significantly affected the ordination scores (2-way ANOVA). Hence, among the habitat variables we recorded, canopy cover appeared to have the strongest overall influence on mammal community structure. Logging intensity, which strongly influenced canopy cover, was also a strong predictor of the ordination scores ( $F_{1,34} = 9.75$ ,  $R^2 = 22.3\%$ ,  $p = 0.004$ ; linear regression; Fig. 4b).

## Discussion

### Roads, Hunting, and Habitat Disturbance

The assemblage of nocturnal species we studied overlaps in only a limited way with that encountered in our earlier investigation (Laurance et al. 2006b), in which daytime surveys of mammal signs and counts were used to infer species abundances in the same study area. Relative to the daytime study, the nocturnal fauna we surveyed was dominated by smaller, often arboreal species; lacked strictly diurnal species, such as monkeys and apes; included some small ungulates but few large species; and provided a larger sample of carnivores.

Our findings here differ in key respects from our earlier findings in a daytime study (Laurance et al. 2006b). First, with the notable exception of rodents (see below), hunting had little impact on mammal community composition (Table 2). Hunters in our study area did sometimes hunt at night, with flashlights and shotguns, especially for ungulates, and the numerous snares they set caught a variety of nocturnal and diurnal species on the ground. Such activities, however, had little impact on the diverse arboreal species that numerically dominated our surveys.

Second, although proximity to roads had a major impact on the species composition of nocturnal mammals, these compositional changes were apparently confined to the vicinity of road margins (Fig. 2). This differs from our daytime survey, which yielded strong evidence of larger-scale declines in species abundance near roads (often extending for many hundreds of meters away from the roads), particularly for ungulates such as elephants, sitatungas, and duikers (Laurance et al. 2006b). Relative to forest transects, road margins had significantly depressed species richness of nocturnal primates, gliding rodents, and small ungulates (Fig. 3) and significantly altered abundances of several mammal guilds and common species (Table 2). These striking differences were largely limited to a zone extending approximately 30 m on either side of road edges. Forest roads have comparably major effects on vertebrate wildlife in the Amazon (Develey & Stouffer



**Table 3.** Significant predictors of mammal-community composition and the abundance of relatively common species within 36 forest transects, with best-subsets and multiple-regression analyses.

Response variable	Multiple-regression models			Significant predictors and their slopes
	F	R <sup>2</sup> (%)	p	
Abundances of mammal guilds				
nocturnal primates	9.50	21.8	0.004	– slope
gliding rodents	3.28	16.6	0.05	+ swamp, + hunting
scansorial rodents <sup>a</sup>	14.65	30.1	0.0005	+ hunting
carnivores	–	–	–	–
smaller ungulates	6.06	15.1	0.019	+ canopy cover
Species richness of mammal guilds				
nocturnal primates	5.61	14.2	0.024	+ topographic position
gliding rodents	4.05	19.7	0.027	+ swamp, + topographic position
carnivores	–	–	–	–
smaller ungulates	13.54	55.9	<0.0001	+ canopy cover, + understory cover, – slope
Abundances of more common species <sup>b</sup>				
Demidoff's galago <sup>a,c</sup>	6.47	16.0	0.016	– slope
Allen's squirrel galago	4.00	10.5	0.054	– understory cover
elegant needle-clawed galago <sup>a</sup>	5.21	24.0	0.011	+ understory cover, – slope
potto <sup>a</sup>	2.92	15.0	0.068	– logging
Cameroon scaly-tail <sup>a</sup>	13.52	28.5	0.0008	+ hunting
brush-tailed porcupine <sup>a</sup>	10.31	38.5	0.0003	+ hunting, + canopy cover
murid rodents <sup>a</sup>	3.26	8.7	0.08	+ hunting
palm civet <sup>a</sup>	4.78	12.3	0.036	+ understory cover
tree hyrax <sup>a</sup>	–	–	–	–
blue duiker	3.40	9.1	0.074	+ canopy cover
Ogilby's duiker <sup>a</sup>	2.89	7.8	0.098	– slope
bay duiker	–	–	–	–
Peter's duiker	5.34	33.4	0.004	+ understory cover, + swampiness, + canopy cover

<sup>a</sup>Data were  $\log(x + 1)$  transformed.<sup>b</sup>Species detected on at least 5 transects.<sup>c</sup>May include Thomas' galagos.

2001; Laurance 2004; Laurance et al. 2004) and tropical Australia (Goosem 1997).

Third, habitat variables and forest disturbance often had a marked influence on the nocturnal fauna (Table 3; Fig. 4). Over half of the most frequently detected species in our study were either negatively associated with logging damage or were significantly influenced by forest canopy or subcanopy cover, both of which were strongly affected by selective logging. Affected species were ecologically diverse, including arboreal mammals (potto, Allen's squirrel galago, elegant needle-clawed galago, palm civet), scansorial species (brush-tailed porcupine), and terrestrial mammals (blue duiker, Peter's duiker). The results of several studies highlight the alarming synergism between logging and overhunting in tropical Africa (e.g., Wilkie et al. 1992, 2000; Milner-Gulland et al. 2003; Elkan et al. 2006), but our findings further emphasize that selective logging alone has important impacts on community composition, even among nocturnal mammals that are little exploited by hunters (see also Malcolm & Ray 2000; White & Tutin 2001; Peters et al. 2006).

That rodents were abundant in hunted forest was a counterintuitive result because some rodents, such as brush-tailed porcupines and marsh cane-rats, are targeted by local hunters, who capture them frequently with snares. The pattern seems robust, however, because overall rodent abundance was significantly higher outside the unhunted oil concession (Table 2) and because hunting intensity was a significant, positive predictor of abundance for 2 rodent guilds and several rodent species (Table 3).

The most plausible explanation for this pattern, we believe, is that the rodents responded positively to habitat changes in or near our study sites in hunted forest. Although all hunted sites were in primary forest, they were located just 0.5–4.5 km from the nearest small village or logging camp (Fig. 1), and these in turn were often adjoined by swidden-farming plots or young regrowth. On average, rodent abundance was 3 times higher within 3 km of human settlements than farther from settlements (0.23 [0.13] vs. 0.08 [0.11] animals/h), a significant difference ( $p = 0.033$ ; Mann-Whitney  $U$ ). Farming plots and regrowth often contain an abundance of fruiting

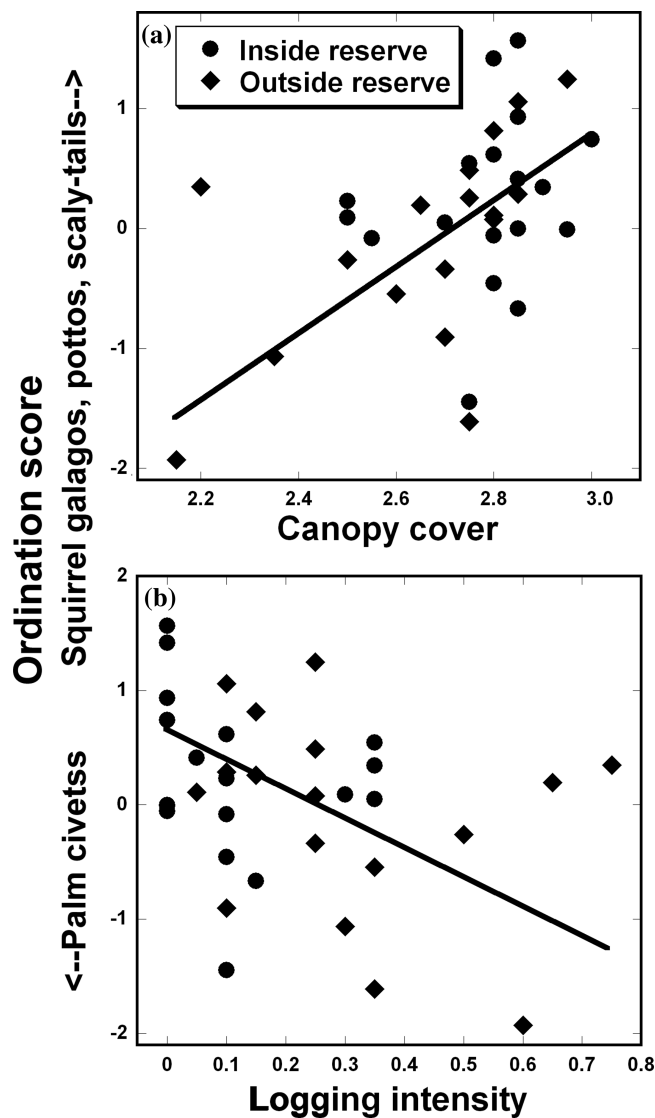


Figure 4. Effects of (a) forest-canopy cover and (b) logging intensity on the structure of nocturnal-mammal assemblages in Gabonese rainforests.

and early-successional plants that are more palatable and less heavily defended by secondary compounds than are plants in primary forest (Robinson & Bennett 2004).

In addition, the hunted sites were more heavily and recently logged on average than those inside the oil concession, resulting in heavier understory cover. Such mosaics of disturbed and primary forest increase the abundance of rodents elsewhere in tropical Africa (Chapman & Chapman 1999; Malcolm & Ray 2000). An alternative possibility is that rodents in hunted areas benefited from reduced predation or competition, which could occur if predators such as carnivorous mammals, raptors, and snakes, or diffuse competitors such as primates and birds, decline in hunted areas. In this study and our earlier day-

time survey (Laurance et al. 2006b), however, we found little evidence of an overall reduction in mammalian carnivores or potential diffuse competitors (diurnal monkeys) in hunted areas, at least under the limited hunting intensities found at our study sites.

### Conservation Implications

Our findings suggest that nocturnal mammals detected by spotlighting in African rainforests, which include many arboreal and smaller (<10 kg) species, are generally less vulnerable to hunting than are larger species such as ungulates and apes. Many nocturnal species were, nonetheless, affected by forest disturbances from roads and selective logging. Species that declined in abundance near roads and in disturbed forest, such as Allen's squirrel galago, potto, blue duiker, and Ogilby's duiker, could be especially vulnerable to forest fragmentation (see also Tutin et al. 1997). Such edge- and disturbance-sensitive species often avoid the matrices of modified habitats surrounding forest fragments (Laurance 1991; Gascon et al. 1999). As a result, their isolated populations in fragments are particularly vulnerable to deleterious genetic and demographic effects, which can be a powerful driving force of local extinction (Shafer 1981; Gilpin & Soulé 1986). These findings are highly relevant to wildlife conservation because forest fragmentation and industrial logging are both expanding rapidly in tropical Africa. Rainforests in West and East Africa have already been severely reduced and fragmented (Naughton-Treves & Weber 2001), and those in Central Africa are projected to be dramatically more fragmented and logged over the next few decades (Laurance et al. 2006a; Zhang et al. 2006; Laporte et al. 2007).

From a regional perspective, the vicinity of our study area at Rabi has special significance because it forms a biogeographic link between the nearby Loango and Moukalaba-Doudou national parks (Fig. 1), among the most important conservation areas in Gabon (Alonso et al. 2006; Laurance et al. 2006a). The Rabi corridor is believed to facilitate seasonal movements of forest elephants and other large wildlife species between inland and coastal areas within the 2 parks (Alonso et al. 2006). As such, it is likely to play a key role in sustaining park biodiversity, by maintaining forest connectivity and by helping to limit the growth of human populations along park borders (cf. Woodroffe & Ginsberg 1998; Brashares et al. 2001). Efforts to further protect this area, possibly as a forest sanctuary under Gabonese law or as part of a larger multiple-use reserve encompassing Rabi oil concession and its adjoining parks, are an urgent priority (Laurance et al. 2006b). Unfortunately, these efforts will become increasingly more difficult over time because road networks for oil and logging operations continue to expand across the greater Rabi area. Newly constructed roads are already facilitating an increase in villages,

slash-and-burn farming, and hunting in the area. Limiting such impacts is imperative if the Rabi area is to continue functioning, and to merit future protection, as a viable wildlife corridor.

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