

# Logging Concessions Can Extend the Conservation Estate for Central African Tropical Forests

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**Abstract:** *The management of tropical forest in timber concessions has been proposed as a solution to prevent further biodiversity loss. The effectiveness of this strategy will likely depend on species-specific, population-level responses to logging. We conducted a survey (749 line transects over 3450 km) in logging concessions (1.2 million ha) in the northern Republic of Congo to examine the impact of logging on large mammal populations, including endangered species such as the elephant (*Loxodonta africana*), gorilla (*Gorilla gorilla*), chimpanzee (*Pan troglodytes*), and bongo (*Tragelaphus eurycerus*). When we estimated species abundance without consideration of transect characteristics, species abundances in logged and unlogged forests were not different for most species. When we modeled the data with a hurdle model approach, however, analyzing species presence and conditional abundance separately with generalized additive models and then combining them to calculate the mean species abundance, species abundance varied strongly depending on transect characteristics. The mean species abundance was often related to the distance to unlogged forest, which suggests that intact forest serves as source habitat for several species. The mean species abundance responded nonlinearly to logging history, changing over 30 years as the forest recovered from logging. Finally the distance away from roads, natural forest clearings, and villages also determined the abundance of mammals. Our results suggest that logged forest can extend the conservation estate for many of Central Africa's most threatened species if managed appropriately. In addition to limiting hunting, logging concessions must be large, contain patches of unlogged forest, and include forest with different logging histories.*

**Keywords:** chimpanzee, elephant, generalized additive model, gorilla, logging concession, Republic of Congo, tropical forest

Las Concesiones Madereras Pueden Extender el Estado de Conservación de los Bosques Tropicales de África Central

**Resumen:** *El manejo de concesiones madereras en bosques tropicales se ha propuesto como una solución para prevenir mayores pérdidas de biodiversidad. La efectividad de esta estrategia probablemente dependerá de las respuestas específicas de las poblaciones a la explotación de madera. Realizamos un muestreo (749 transectos de línea en 3450 km) en concesiones madereras (1.2 millones de ha) en el norte de la República de Congo para examinar el impacto de la explotación de madera sobre las poblaciones de mamíferos mayores, incluyendo especies en peligro como el elefante (*Loxodonta africana*), el gorila (*Gorilla gorilla*), el chimpancé (*Pan troglodytes*) y el bongo (*Tragelaphus eurycerus*). Cuando estimamos la abundancia de especies sin considerar las características del transecto, la abundancia de especies en bosques talados y no talados no fue diferente para la mayoría de las especies. Sin embargo, cuando modelamos los datos con un modelo de obstáculos, en el que analizamos la presencia de las especies y la abundancia condicional por separado, la abundancia de las especies varió poderosamente dependiendo de las características del transecto. La abundancia promedio de las especies a menudo se relacionó con la distancia a un bosque no talado, lo que sugiere que el bosque intacto funciona como un hábitat fuente para varias especies. La abundancia*

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*promedio de las especies respondió no linealmente a la historia de explotación, presentando cambios en 30 años a medida que el bosque se recuperó de la tala. Finalmente, la distancia a los caminos, los claros naturales en el bosque y a las aldeas también determinó la abundancia de los mamíferos. Nuestros resultados sugieren que los bosques talados pueden extender el estado de conservación de muchas de las especies más amenazadas en África Central si son manejados adecuadamente. Adicionalmente a la limitación de la cacería, las concesiones madereras deben ser extensas, contener parches de bosque no talado e incluir bosques con diferentes historias de explotación.*

**Palabras Clave:** bosque tropical, chimpancé, concesión maderera, elefante, gorila, modelo aditivo generalizado, República de Congo

## Introduction

The limited area, number, and distribution of protected areas in the tropics render them inadequate to prevent continued biodiversity loss (Soulé & Sanjayan 1998; Fagan et al. 2006). Consequently conservationists seek and test additional strategies to protect tropical forest diversity outside parks and reserves (Ferraro & Kiss 2002; Pearce et al. 2003). The need for new strategies is underscored by the fact that most tropical forests lie in developing nations, where poor governance and corruption threaten protected areas, poverty often pushes people to overexploit forest resources to improve their livelihoods, and governments depend on extractive industries such as oil production and logging to generate revenue (Barrett et al. 2001; Milner-Gulland et al. 2003; Smith et al. 2003).

Logging is among the most extensive extractive activities across the tropics. Of Central Africa's remaining forests 30–40% fall within commercial logging concessions (Laporte et al. 2007), and as oil stocks dwindle, timber production is forecast to increase in economic importance across the Congo Basin (Trebaol & Chaillol 2002). Given these economic realities and the accelerating rate at which forests are being opened for logging, the conservation of tropical forests may depend less on identifying new protected areas and more on understanding under what conditions logging can be compatible with conservation goals.

The conservation value of degraded forest depends on how logging affects forest biodiversity (Brook et al. 2006; Wright & Muller-Landau 2006a, 2006b). Despite a multitude of studies, generalizable results are lacking because of differences in study methods, logging techniques (logging intensities), historical characteristics (time since logging), and species-specific responses to logging disturbance (reviewed by Putz et al. 2000). Results of studies are often inconsistent: increased and decreased abundance and diversity in response to logging have been reported (e.g. Azevedo-Ramos et al. 2006; Meijaard et al. 2006; Cleary et al. 2007). Such disparities make existing research difficult to interpret and almost impossible to translate into cohesive conservation policy and practice.

To further complicate the issue, direct effects of logging (alteration of forest structure and increased fragmentation) on animal populations and biodiversity are often confounded by indirect effects (hunting, disease transmission, and deforestation for agriculture). The opening of forests to logging sets off a domino effect of road construction, immigration of job seekers, and an escalation of commercial hunting and trade (Wilkie et al. 2000; Fa et al. 2005). In fact the harvest of wildlife may more strongly contribute to biodiversity loss than the harvest of trees for timber (Milner-Gulland et al. 2003). In the Congo Basin approximately 60% of vertebrate game species are overharvested (Fa et al. 2002).

One proposed solution to mitigate biodiversity loss in tropical forests is to integrate production forests into existing conservation strategies (Rice et al. 1997; Chazdon 1998; Pearce et al. 2003). The idea is that if properly managed, the large size and varied habitats of logging concessions could complement the existing system of protected areas, enlarging the "conservation estate" (Putz et al. 2001). In recent years numerous forestry companies have adopted a paradigm of sustainable forest management that, in theory, promotes biodiversity conservation (ITTO 2005; FSC 2006). But given our limited understanding of how logging affects biodiversity, the idea that production forests can meet both forestry and conservation goals should be tested before limited conservation resources are invested in logging concessions (Bawa & Seidler 1998).

Our goal was to determine to what degree production forests might serve to extend the conservation estate in Central Africa by an examination of the impact of selective logging on large mammal populations. We conducted surveys in logged and unlogged forests over a large spatial scale (1.2 million ha) to examine the direct impact of logging on abundances of large mammals, investigate whether the spatial structure and temporal characteristics of concessions determine the abundance of mammal species, decouple the direct and indirect effects of logging on mammal populations, and develop management recommendations for the conservation of wildlife in tropical logging concessions.

## Methods

### Study Area

We conducted the study in four logging concessions (Kabo, Pokola, Loundougou, and Toukoulaka) adjacent to the Sangha trinational network of protected areas and the Nouabalé-Ndoki National Park (NNNP) in the northern Republic of Congo (see Supporting Information). These tropical forests are rich in flora and fauna, include several different forest types, and are characterized by large natural clearings that provide water and minerals to animals. To decrease the impact of logging on the NNNP the Wildlife Conservation Society (WCS) is working with the logging company, Congolaise Industrielle des Bois (CIB), and the Government of Congo (GOC) to improve forestry and wildlife management in the concessions (Elkan et al. 2006). Our study was conducted during the early phases (2001–2002) of the project (Buffer Zone Project [BZP]) to (1) create a baseline to inform the development of concession management plans and (2) understand factors that influence large mammal abundances and distributions so that the project's success could be evaluated over time. Because the study was conducted when conservation activities were just beginning, the results reflect the direct and indirect impacts of logging and not of the management actions.

Logging history in the area extends back to 30 years. When CIB gained concessionary rights to the area in 1997, the concessions included unlogged and logged forest areas. At the time of the study none of the forests had been logged a second time, although CIB has since started a second logging rotation based on a 30-year cycle (CIB 2006). Thus, the study site had a variety of forest types, logging histories (time since logging), and human population densities (Table 1). Similar logging techniques were used among years; timber extraction was low in intensity (<2.5 trees/ha) and selective in nature (Table 1; CIB 2006).

### Survey Methods

In 2001 and 2002 we surveyed the concessions for large mammal species (listed in Table 2). The surveys were

conducted throughout the year along transects initially established for a concurrent inventory of timber species. Inventory lines were opened in parallel from west to east across the concessions, separated latitudinally by 2.5-km intervals, and cut primarily through mixed tropical forest, where logging was to be conducted. *Gilbertiodendron* and swamp forest were thus undersampled relative to their actual representation. Three field teams walked the inventory lines to survey for mammals several weeks after the tree inventories. The inventory lines were divided into 5-km transects separated by approximately 5 km. The field teams were randomly assigned the inventory lines to minimize observer bias among the teams.

The field teams used a distance sampling method (Buckland et al. 2001). A surveyor slowly walked the transects while scanning the ground and forest for animals and their sign. The distance along the transects was measured to the nearest meter, and the distance from the transect centerline to the center of each dung pile and ape nest was measured to the nearest centimeter. We classified ape nest sites to species as in Poulsen and Clark (2004). Because animal sign was easier to detect than live animals, we present results on dung piles for elephants and ungulates, nests for apes, and direct observations of monkey groups (Table 2).

### Estimation of Animal Density

We estimated mammal densities (observations per square kilometer) in logged and unlogged forests and calculated their associated coefficients of variation (CV) and 95% confidence intervals (CIs) with Distance 5.0 software (Table 2; Buckland et al. 2001; Thomas et al. 2006). Because the number of observations of bongo dung was low and perpendicular distances from the transects to monkey groups were not measured, we calculated relative abundances (observations per kilometer) for those species. We use *abundance* to refer to either density or relative abundance.

When estimating densities with Distance 5.0 we truncated the observations farthest from each transect to ensure robust estimation of detection and an effective strip half-width (Buckland et al. 2001). We fitted detection

**Table 1.** Survey sampling effort and details about logging intensity, history, human population, and density of roads in the four logging concessions.

Concession	Area (km <sup>2</sup> )	Transect effort (km)	No. of transects	Year first logged	Avg. logging intensity (m <sup>3</sup> /km <sup>2</sup> )	Yearly offtake* (m <sup>3</sup> )	Human population	No. of villages	Road density (km/km <sup>2</sup> )
Kabo	2,670	758	161	1968	21.6	133,942	4,222	7	1.07
Loundougou	3,900	895	186	2002	23.2	163,427	2,693	17	0.20
Pokola	3,775	1187	59	1968	24.1	144,901	16,299	13	1.08
Toukoulaka	1,625	610	149	1992	28.3	137,455	1,357	4	1.72
Total	11,970	3450	749				24,571	41	

\**Entandophragma cylindricum*, *E. utile*, *Triplochiton scleroxylon*, and *Milicia excelsa* make up approximately 90% of the total volume logged in Kabo, Pokola, and Toukoulaka (CIB 2006). In 2005 the Loundougou and Toukoulaka concessions were merged as a single concession.

Table 2. Abundances of mammal species in logged and unlogged forest in four logging concessions estimated with Distance 5.0.

Species	Forest type	Measure of abundance	Abundance (95% CIs) <sup>a</sup>	df	CV (%)
Blue duiker	unlogged	density of dung	316.6 <sup>†</sup> (162.1–618.5)	162.1	34.9
<i>Cephalophus monticola</i>	logged		154.7 <sup>†</sup> (79.1–302.5)	79.1	35.0
Bongo	unlogged	rel. abund. of dung	0.003 <sup>‡</sup> (–0.04–0.04)		
<i>Tragelaphus eurycerus</i>	logged		0.01 <sup>‡</sup> (–0.04–0.06)		
Buffalo	unlogged	density of dung	NA		
<i>Syncerus cafer</i>	logged		51.5 <sup>†</sup> (28.6–92.6)	134.9	30.4
Chimpanzee <sup>b</sup>	unlogged	density of individuals	0.29 <sup>†</sup> (0.23–0.36)	287.8	10.9
<i>Pan troglodytes</i>	logged		0.24 <sup>†</sup> (0.20–0.28)	560.0	8.6
Elephant <sup>c</sup>	unlogged	density of individuals	0.38 <sup>†</sup> (0.29–0.49)	165.9	13.7
<i>Loxodonta africana</i>	logged		0.57 <sup>†</sup> (0.47–0.70)	334.3	10.1
Gorilla <sup>b</sup>	unlogged	density of individuals	1.92 <sup>†</sup> (1.36–2.71)	204.6	17.6
<i>Gorilla gorilla</i>	logged		1.57 <sup>†</sup> (1.27–1.94)	537.4	11.0
Guenon	unlogged	rel. abund. of groups	0.16 <sup>‡</sup> (0.14–0.18)		
<i>Cercopithecus nictitans</i>	logged		0.15 <sup>‡</sup> (0.14–0.16)		
Mangabey	unlogged	rel. abund. of groups	0.15 <sup>‡</sup> (0.13–0.17)		
<i>Lophocebus albigena</i>	logged		0.12 <sup>‡</sup> (0.11–0.13)		
Medium-sized duikers <sup>d</sup>	unlogged	density of dung	1287.0 <sup>†</sup> (986.5–679.2)	161.2	13.5
<i>Cephalophus</i> spp.	logged		1706.2 <sup>†</sup> (269.5–1418.2)	269.5	9.4
Yellow-backed duiker	unlogged	density of dung	295.3 <sup>†</sup> (211.3–412.5)	420.8	17.1
<i>Cephalophus silvicultor</i>	logged		411.0 <sup>†</sup> (333.9–505.9)	333.9	10.6

<sup>a</sup>Abundances were estimated from dung piles for forest elephant, forest buffalo, bongo, and duikers (blue duiker, medium-sized duikers, and yellow-backed duiker), from nests for gorilla and chimpanzee, and from direct observations for monkeys (guenon and mangabey). Measure of abundance (density or relative abundance) differs among species. Unit of measurement: <sup>†</sup>, per square kilometer; <sup>‡</sup>, per kilometer.

<sup>b</sup>Density of ape nests converted to gorilla and chimpanzee densities with nest decay rates (91.5 days, SE 1.67) from the Goulougou Triangle, which is adjacent to the Kabo concession, and assuming production of one nest per night (Morgan et al. 2006). Average group size based on the number of nests in fresh and recent nest groups (gorilla = 2.81 nests/group, chimpanzee = 1.68 nests/group). We assumed these rates do not vary among sites.

<sup>c</sup>We used estimates of 19 defecations per day and dung lifespan of 45 days to translate dung densities into densities of individual animals (Barnes 2001).

<sup>d</sup>Dung cannot reliably be distinguished by species, so medium-sized duikers include *Cephalophus leucogaster*, *C. nigrifrons*, *C. dorsalis*, and *C. callipygus*.

functions to the data sequentially with half-normal, uniform, and hazard rate key functions that contained cosine, hermite polynomial, and simple polynomial adjustment terms (Buckland et al. 2001). The best model was selected on the basis of the lowest Akaike information criterion (AIC) score. Model fit was examined with chi-square goodness-of-fit tests.

### Direct and Indirect Effects of Logging on Wildlife Populations

To decouple the direct and indirect effects of logging on animal populations we related the presence and abundance of each species to habitat, distance from forest clearings, logged versus unlogged forest, time since logging, distance from unlogged forest, distance from primary roads, human population density, and hunting intensity. We characterized each transect according to these explanatory variables. We used ArcView 3.2 (ESRI, Redlands, California) to assign values from existing maps of habitat and logging history. The habitat categories included open-canopy forest, closed-canopy forest, *Gilbertiodendron* forest, Marantaceae forest, and swamp forest. We calculated the distance (kilometers) from the centroid of each transect to the nearest primary road, nearest forest clearing, and nearest patch of unlogged forest. Human

population density was estimated as the number of people living in camps and villages within 10 km of each transect. We first modeled the animal data (see below) to estimate the effect of logging by including all explanatory variables (except time since logging) and by treating logging as a discrete factor (logged vs. unlogged forest). Then we examined the effect of time since logging by modeling only the data from logged forest, including all explanatory variables, and by treating time since logging as a continuous variable.

As is common in animal surveys, many transects lacked observations for one or more species; thus, the data set included too many zeros to meet the statistical assumptions of standard error distributions (e.g., Poisson and negative binomial) for modeling animal abundance. To accommodate this data structure we used a two-part hurdle model to first estimate species presence and then species abundance if the species was present (Martin et al. 2005). We estimated the mean abundance for each level of the response variables by multiplying the binomial proportion (probability of species presence,  $\psi$ ) by the conditional mean (conditional abundance,  $\lambda$ ):

$$N_i = \psi_i \times \lambda_i,$$

$$\text{pres}_i \sim \text{Bernoulli}(\psi_i),$$

$$K_i \sim \text{Poisson}(\lambda_i),$$

where  $N_i$  is mean abundance for species  $i$ ,  $\text{pres}_i$  is a binary value indicating whether or not species  $i$  is present, and  $K_i$  is its realized abundance if species  $i$  is present. If  $\lambda_i$  is overdispersed,  $\text{var}(\lambda_i) \gg \text{mean}(\lambda_i)$ , then a quasi-Poisson model can be used if the variance is rescaled as  $\theta\lambda_i$ , where  $\theta$  is the overdispersion parameter.

With inclusion of explanatory variables, generalized linear modeling (GLMs) can be used to explain variation in  $\psi_i$  and  $\lambda_i$ . We modeled the animal data with generalized additive models (GAMs), an extension of generalized linear models that provide a technique to fit a smooth relationship between one or more explanatory variables and a response variable (Wood 2006). With GAMs nonlinear effects can be modeled without manually specifying their precise form. We fit GAMs to species presence data with a binomial error distribution and logit transformation and to conditional abundance data with a quasi-Poisson distribution to account for overdispersion with a log link. Both models included an offset to adjust for between-transect differences in sampling effort (Agresti 1996). The models were fit in R version 2.7.1 (R Development Core Team 2008) with the *mgcv* package (Wood 2006; see Supporting Information for model equations and details).

In preliminary analyses no single model clearly fit species-specific data better than the others, and stepwise model selection chose different models depending on the direction of the selection procedure (Whittingham et al. 2006). Therefore we averaged the models to reduce model selection bias and account for model selection uncertainty (Burnham & Anderson 2002). We fitted GAM models to all possible combinations of explanatory variables (127 candidate models) and averaged models and parameters for models within six QAIC units of the model with the lowest QAIC score (Burnham & Anderson 2002) in the *dRedging* package (K. Bartón 2008) QAIC (quasi-AIC) is a variant of the Akaike Information Criterion for over-dispersed data. We used a cutoff of six QAIC points because lower cutoffs sometimes miss the most parsimonious model when data are overdispersed (Richards 2008).

We calculated the mean abundance of each species for each explanatory variable by multiplying the probability of presence by the conditional abundance of the species estimated from the averaged GAM models. All auxiliary variables were held at their mean levels, and habitat was held as closed-canopy forest. Standard errors of the mean abundance were estimated with the formula for variance of the product of two random variables to produce CIs (Goodman 1960).

As in most large observational studies our models identified the explanatory variables that determined animal abundance and accurately estimated their mean effects, but they did not provide precise predictions of animal abundance for any single transect (Supporting Information). We estimated biological effects through model parameters, rather than by hypothesis testing. To avoid confusion we use the term *distinguishable* (rather than *significant*) to refer to the situation in which CIs of parameter estimates do not overlap zero or other parameters.

## Results

### Species Abundance in Logged and Unlogged Forests

The field teams walked 749 transects (3450 km in total) (Table 1). For most species we identified no difference in the abundance between logged and unlogged forests: CIs of abundance estimates usually overlapped considerably (Table 2). The lack of observations of buffalo in unlogged forest and the slightly overlapping CIs for elephants suggest that these species may have greater densities in logged forest. Nevertheless, these results represent the combined effects of all explanatory variables (and unmeasured variables) on species abundance and provide little insight into the relative effects of logging, hunting pressure, or spatial structure of the landscape.

### Direct and Indirect Effects of Logging on Wildlife

Logging contributed to species presence for 10 species and to conditional abundance for 7 (Table 3). Buffalo presence (effect = 0.70, 95% CI = 0.18–1.23), chimpanzee conditional abundance (effect = 0.74, 95% CI = 0.07–1.41), yellow-backed duiker presence (effect = 0.42, 95% CI = 0.03–0.81), elephant presence (effect = 0.87, 95% CI = 0.31–1.44), and gorilla presence (effect = 0.97, 95% CI = 0.45–1.48) were distinguishably greater in logged than in unlogged forests, but gorilla conditional abundance (effect =  $-0.62$ ; 95% CI =  $-0.93$  to  $-0.32$ ) decreased in logged forests. The mean species abundance in logged forest was distinguishably higher than in unlogged forest for elephant, gorilla, and medium-sized duiker, whereas the mean abundances of other species did not differ between the forest types (Fig. 1).

To examine the effect of logging history, human pressure, and landscape characteristics on species presence and conditional abundance in logged forests, we refit the models for all logged transects and determined the important explanatory variables by model averaging. The variables that predicted species presence and conditional abundance varied by species, although distance to

Table 3. Explanatory variables included in models of species presence and conditional abundance.\*

Species	Covariates	
	presence	conditional abundance
Blue duiker	Int (−7.88: −8.24 to −7.52), sPop, sYL, Unlog (0.07: 0.03–0.11)	Int (−0.47: −0.72 to −0.22), Clear, Hunt, Road, sPop, Unlog
Bongo	Int (0.70: 0.43–0.96), sClear, Road, Unlog (−0.07: −0.10 to −0.04)	Int (−0.55: −0.62 to −0.47), sRoad
Buffalo	Int (0.57: 0.24–0.90), Hab, sClear, Unlog (−0.06: −0.10 to −0.03), YL	Int (−0.54: −0.63 to −0.44), Clear, sPop
Chimpanzee	Int (0.68: 0.19–1.38), Hab, Hunt (−0.19: −0.28 to −0.04), Pop, sClear, Unlog (−0.08: −0.11 to −0.05)	Int (−0.65: −0.77 to −0.53), Hunt, sClear, sRoad, YL (0.01: 0.001–0.02)
Elephant	Int (0.79: 0.50–2.24), Hab, Hunt (−0.20: −0.33 to −0.07), sClear, sPop, sRoad, sYL, Unlog (−0.06: −0.09 to −0.002)	Int (−0.40: −0.52 to −0.28), Hab, Hunt (−0.12: −0.19 to −0.05), sClear, sPop, sYL, Unlog (−0.02: −0.04 to −0.004)
Gorilla	Int (−10.82: −11.22 to −10.41), Unlog (0.12: 0.07–0.17), sClear, sRoad, sYL	Int (−0.47: −0.58 to −0.37), sRoad, sYL, Unlog (−0.02: −0.03 to −0.001)
Guenon	Int (0.67: 0.45–0.90), Hab, Hunt (−0.30: −0.43 to −0.17), sPop, sYL, Unlog (−0.03: −0.06 to −0.01)	Int (−0.46: −0.58 to −0.33), Clear, sPop, sYL, Unlog (−0.02: −0.03 to −0.001)
Mangabey	Int, sClear, Unlog, YL (0.02: 0.005–0.04)	Int (−7.89: −8.11 to −7.67), Hab, Unlog (−0.03: −0.05 to −0.02), sRoad
Medium-sized duiker	Int (0.47: 0.08–0.87), Clear, Pop, Road, sYL, Unlog (−0.04: −0.07 to −0.01)	Int (−34: −0.51 to −0.16), Clear, Hab, Hunt (−0.12: −0.20 to −0.05), sPop, sRoad, sYL, Unlog (−0.02: −0.04 to −0.003)
Yellow-backed duiker	Int (−7.24: −7.59 to −6.89), Unlog (0.08: 0.04, 0.12), sPop, sYL	Int (−0.40: −0.59 to −0.21), Clear, Hab, sPop, sYL, Unlog (−0.03: −0.04 to −0.01)
Occurrence of explanatory variables in models for all species	YL 8, Pop 6, Unlog, 10, Road 4, Clear 7, Hab 4, Hunt 4	YL 6, Pop 6, Unlog 7, Road 6, Clear 7, Hab 4, Hunt 4

\*Abbreviations: Int, intercept; Hab, habitat; Pop, population (per 100 people); Road, distance from primary roads; Clear, distance from forest clearings; Unlog, distance from unlogged forest; YL, year logged; Hunt, hunting sign; s, smoothed parameters (e.g., sRoad). Nonsmoothed explanatory variables with effects distinguishably different from zero are presented with effect size and 95% CI.

unlogged forest and time since logging were consistently important (Table 3).

#### EXPLANATORY VARIABLES

Habitat was retained in fewer models of the presence and conditional abundance than most other explanatory variables. The lesser importance of habitat in explaining animal abundance, and the lack of distinguishable differences among habitats (Table 3), may partially be a result of the study design, which focused on open- and closed-canopy forests (70% of all transects) where logging was conducted. Greater sampling in other habitats may have resulted in the detection of more marked differences in animal abundance among the habitat types.

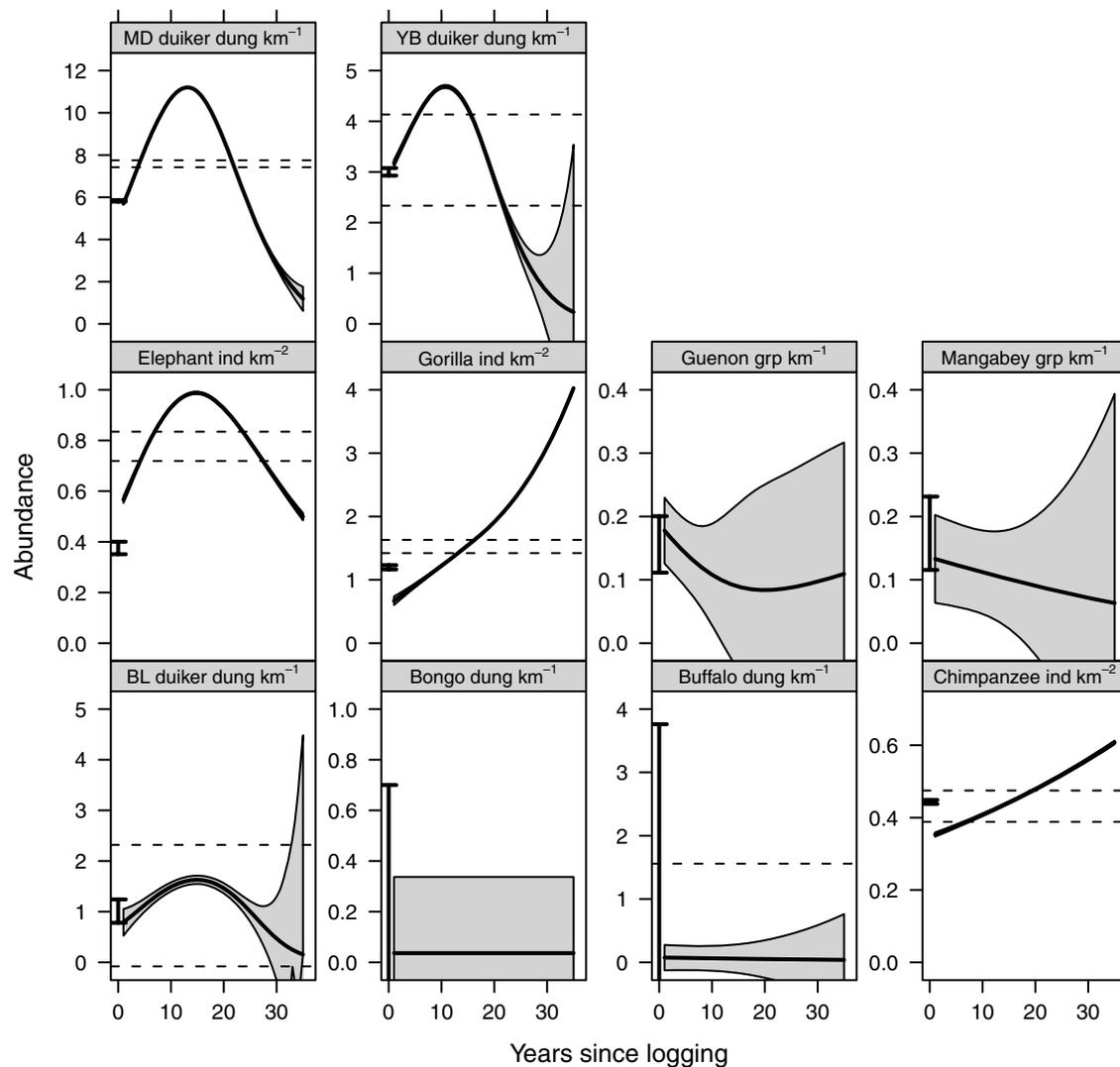
Natural forest clearings (referred to as *bais*), however, strongly influenced the mean abundance of ungulates. The mean abundances of duikers and elephants were greater near forest clearings, with elephant mean abundances decreasing by nearly 75% 15 km away (Table 3; Fig. 3). Primate mean abundance, particularly ape abundance, increased with distance from clearings.

Most species demonstrated nonlinear responses to logging over time (Table 3; Fig. 2). The mean abundances of

apes declined immediately after logging, but recovered over time and surpassed the abundances in unlogged forest after 10–20 years. The mean abundances of arboreal monkeys (guenon, *Cercopithecus* spp.) and mangabey (*Lophocebus* sp.) declined after logging. The mean abundances of duikers increased for the first 10–15 years after logging, after which the abundance fell dramatically. Like duikers, elephant abundance increased for approximately 15–20 years after logging and then returned to an abundance similar to that observed immediately after logging, which was higher than in unlogged forest. Bongo and buffalo abundances did not respond strongly to logging.

The presence and conditional abundance of most species decreased distinguishably with distance from unlogged forest (Table 3). When the presence and conditional abundance were combined, the mean species abundance increased with distance from unlogged forest for gorilla, chimpanzee, and blue duiker and decreased for the rest of the species (Fig. 4). Thus unlogged forest likely serves as a source habitat for most duikers, monkeys, bongo, buffalo, and elephant.

Proximity to roads strongly and negatively affected apes and elephants. Gorilla mean abundance was nearly



**Figure 1.** Mean abundance of species as a function of time since logging. Units differ among species (MD, medium; dung, dung pile; YB, yellow-backed; ind, individuals; grp, animal groups; BL, blue), as do the measures of abundance (gray shading, confidence intervals [CIs]; points and bars at year zero, abundance and 95% CI of species in unlogged forest; dashed horizontal lines, 95% CI for average mean abundance across all distances from clearings [If these lines are absent, CI for that species is very broad and outside the plot.]

six times lower at roads than 30 km away. Elephant abundance increased up to 10–15 km from roads, after which its mean abundance stabilized (Table 3; Fig. 4). The mean abundance of mangabeys increased, although less dramatically, with distance from roads. Blue and medium-sized duiker abundances were greater near roads, but roads did not have a strong effect on the mean abundances of guenon, yellow-backed duiker, bongo, or buffalo.

Hunting intensity (hunting sign per kilometer) was distinguishably and negatively related to species presence for bongo, chimpanzee, guenon, and elephant and to conditional abundance for medium-sized duikers and elephants (Table 3; Supporting Information). Increases in hunting sign resulted in decreased mean abundance for elephants and medium-sized duikers.

Other species did not demonstrate a strong response to hunting.

The median number of people within 10 km of the transects was 279 (0.89 people/km<sup>2</sup>), and the maximum was 7184 (22.88 people/km<sup>2</sup>). Of 22 settlements only one village had a population over 2000 people; therefore, we examined the effect of population on the mean abundance up to this limit. Gorillas, bongo, buffalos, and mangabeys were not affected by this relatively low human population; they showed no variation in the mean abundance (Supporting Information). The mean chimpanzee and guenon abundances decreased with population density around the transects. Elephant mean abundance increased with population density, reaching a mean abundance three times higher at 2000 people than

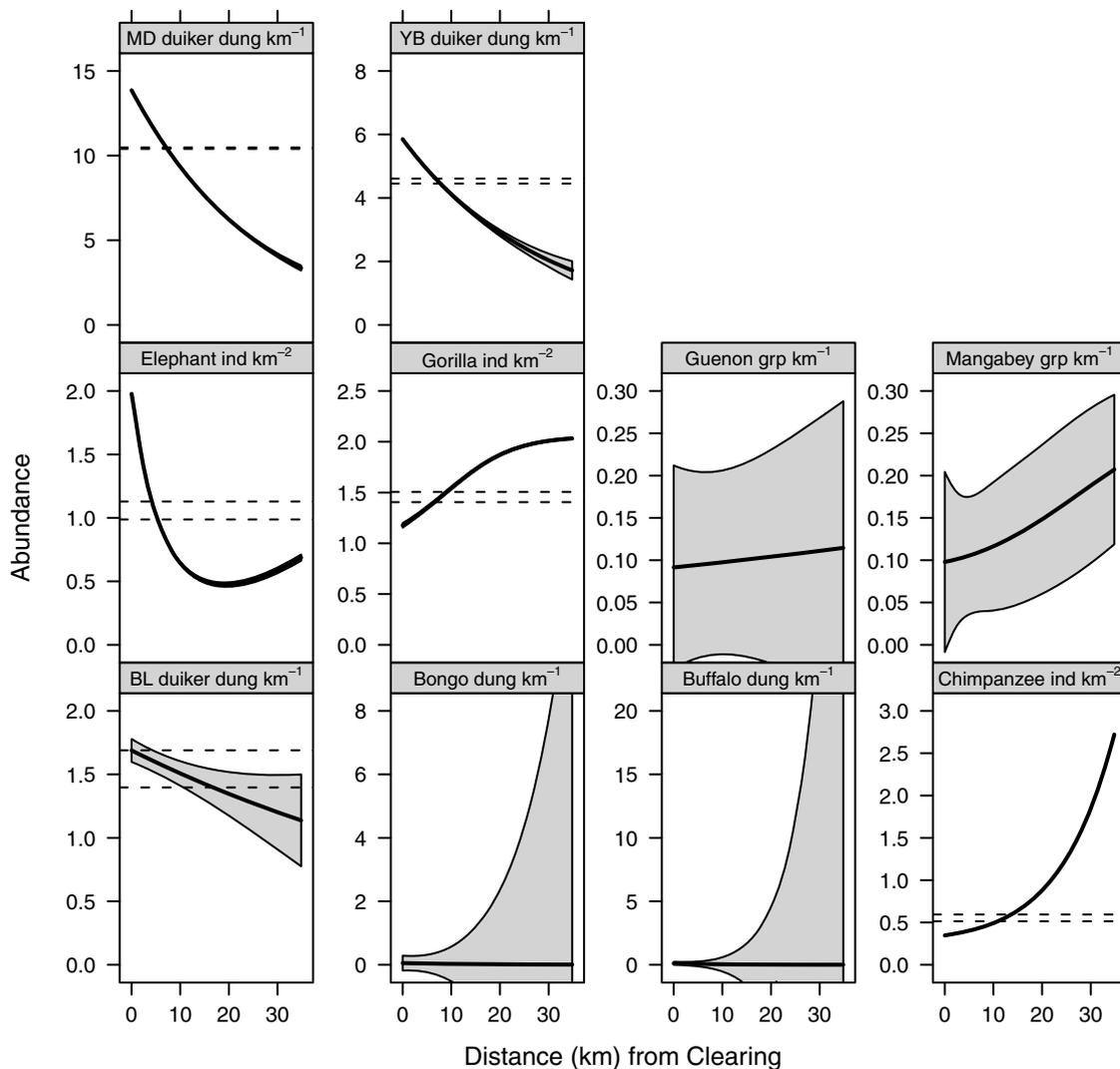


Figure 2. Mean abundance of species as a function of distance from forest clearings. See legend of Fig. 1 for explanation of units and measures of abundance and definitions of abbreviations.

in unpopulated forest. Duiker abundances increased with human population densities relative to other species, reaching peak abundances at around 1000–1500 people, after which the mean abundances declined.

## Discussion

The conservation value of degraded and secondary forests has been at the center of a debate over the future of tropical forest species. Wright and Muller-Landau (2006a, 2006b) argue that secondary forests could rescue species unlikely to persist in small remnants of primary forest, whereas Brook et al. (2006) believe tropical secondary forests support lower biodiversity, have a predominance of generalist species, and act as reproductive sinks. Our results provide evidence that forests

degraded by logging can enlarge the conservation estate for several species of large mammals. Despite the high canopy damage and edge effects associated with selective logging (Johns et al. 1996; Laurance 2000), we found that managed production forest supported by nearby unlogged forest did not have significantly lower abundances of large mammals than unlogged forest. The abundance of large mammals in the four tropical logging concessions even rivaled that of the adjacent Nouabalé-Ndoki National Park (Stokes 2007). Even so, some species (primates and blue duiker) tended to be less abundant in logged than in unlogged forest, and animal populations need to be monitored as logging continues and human population grows.

The mean species abundance varied strongly across logging concessions with changes in logging history, hunting intensity, and proximity to roads, clearings, and unlogged forest. Species abundance responded to logging

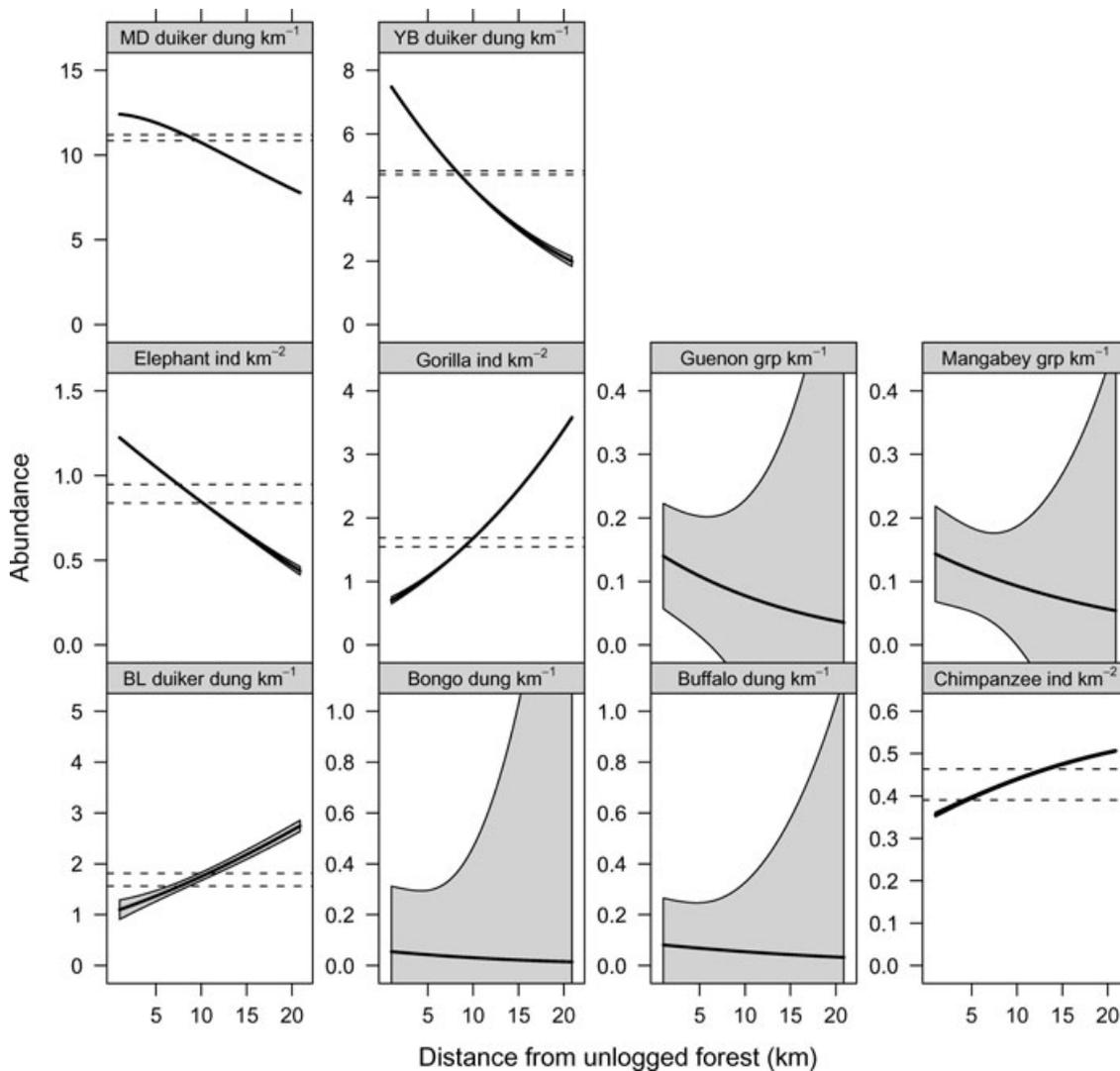


Figure 3. Mean abundance of species as a function of distance from unlogged forest. See Fig. 1 legend for explanation of units and measures of abundance and definitions of abbreviations.

history, changing over 30 years as the forest recovered from logging. The indirect effects of logging, such as proximity to roads, hunting, and human occupation, differentially influenced the patterns of species abundance. Finally species abundance was strongly related to the distance to unlogged forest for several species, which suggests that intact forest may serve as source habitat. Thus managed forests may be especially valuable when they are adjacent to or surround protected areas (Lamb et al. 2005), assuming that hunting regulations are enforced (Naughton-Treves et al. 2003).

In addition to highlighting the direct and indirect effects of logging that most affect large mammal abundances, our results demonstrate that species presence and conditional abundance are frequently driven by different processes, and animal abundance responds nonlinearly to the temporal and spatial effects of logging. Thus improving our understanding of how logging in-

fluences species abundance will require that we move beyond conventional linear approaches to model these relationships.

#### Direct and Indirect Effects of Logging on Wildlife

The relationship between abundance and logging history varied by species and changed over time. The nonlinear responses to logging suggest that animal abundance varies with different stages of forest regrowth and may explain contradictory results among previous studies. Studies conducted in a single time period after logging are essentially snapshots of a population and ignore a sequence of population-level responses to changes in the forest. This complex relationship between time since logging and abundance will be further confounded as logging companies begin second and third rotation cycles.

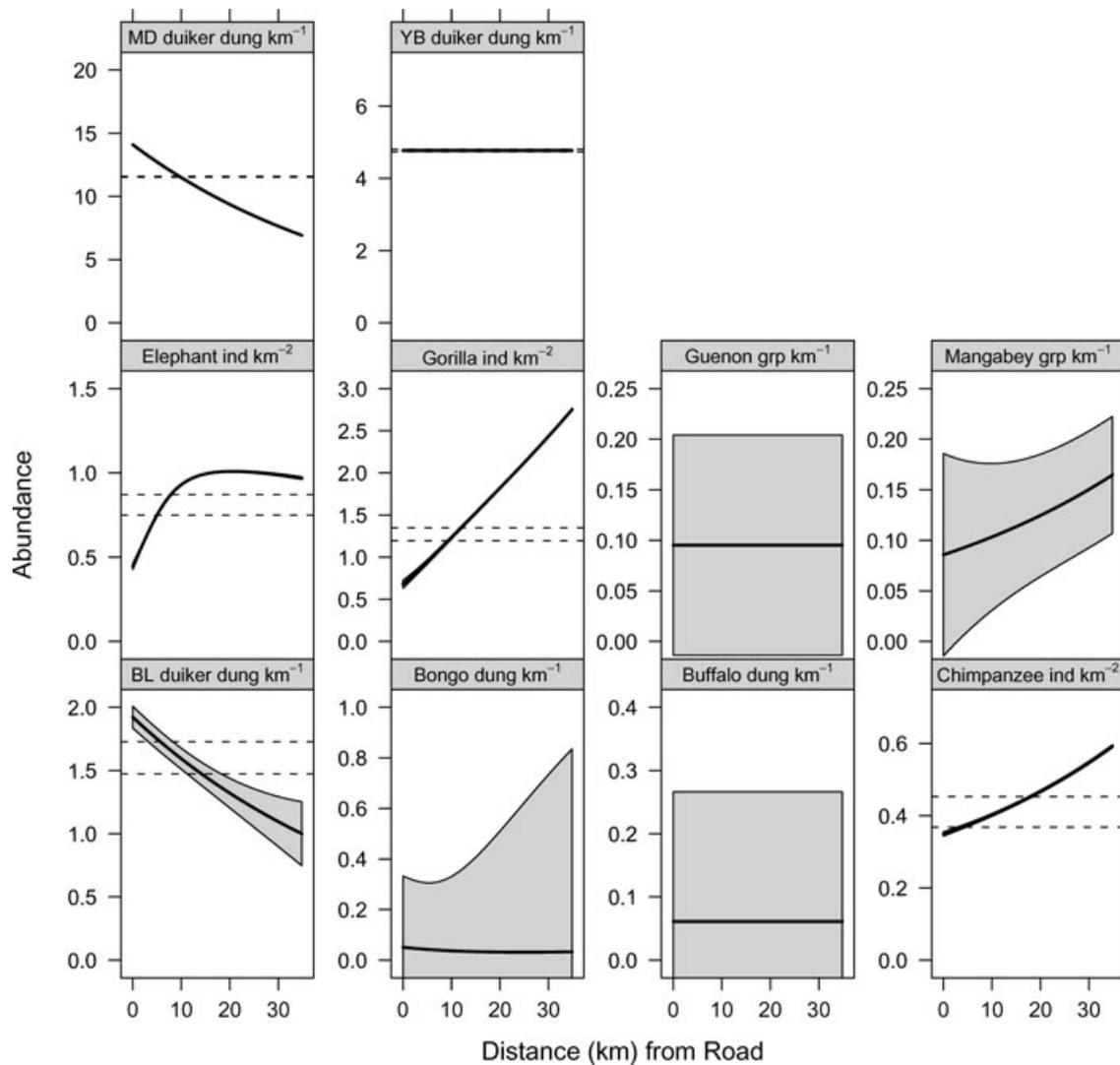


Figure 4. Mean abundance of species as a function of distance from primary roads. See Fig. 1 legend for explanation of units and measures of abundance and definitions of abbreviations.

Changes in animal abundance over time after logging can be explained by shifts in forest structure related to reduction of canopy cover, which generally creates a surge of new growth of grasses, shrubs, and herbs on the forest floor (Heydon & Bulloh 1997; Malcolm & Ray 2000). For several years following logging, wildlife experiences a net movement of resources to lower levels of the forest strata, which benefits terrestrial and semiterrestrial species. Resource gradients gradually shift back toward the upper strata as pioneer trees and saplings are released from the understory and fill canopy gaps, resulting in the return of understory vegetation resources to levels more closely resembling unlogged forests. Vertical shifts in forest resource gradients likely explain the observed changes in animal abundances over time.

Natural forest clearings (bais), unlike other habitat variables included in our models, strongly influenced the

distribution and abundance of forest elephants and other ungulate species. Bais are canopy openings characterized by grasses, herbs, and browse that can attract high numbers of herbivores and browsers by providing locally high abundances of forage, minerals, and water (Klaus et al. 1998; Magliocca & Gautier-Hion 2002). Such patchily distributed resources may disproportionately influence the movement and spatial distribution of large mammals, particularly elephants, and should be protected from degradation during logging operations (Blake & Inkamba-Nkulu 2004).

Throughout Central Africa, roads are considered deleterious for wildlife. Road construction limits the physical movement of some species (Laurance et al. 2006) and is accompanied by increased hunting, unplanned colonization, and deforestation or forest degradation (Wilkie et al. 2000; Blake et al. 2007). Species responses

to these indirect impacts of logging can be obscured by the fact that they occur in concert and may have opposite effects. For example, disturbance of habitat around settlements (e.g., agriculture) can increase resource availability and thus increase the productivity and abundance of some species. At the same time hunting would decrease the abundance of many of these species, depending on their legal status (i.e., elephants may not be hunted next to villages where poachers could be apprehended). Finally some species may avoid roads even in the absence of strong hunting pressure. We attempted to decouple these factors by including indexes of hunting, colonization, and roads directly into our statistical models.

Medium-sized duikers responded well to habitat disturbance, increasing in abundance in logged areas, along roads, and near small villages (where clearing and burning for crops may increase resources). Duiker abundance decreased around villages with over 1000 people, which may be the point at which hunting pressure overrides the positive effects of habitat alteration. A hunting study conducted concurrently with our surveys found no evidence of overharvesting in two villages (<1500 people; Eaton 2002). Trends may have changed with the expansion of logging and population growth in the concessions (Poulsen et al. 2007).

Similarly chimpanzees and guenons were negatively affected by population density and roads, but not by hunting. These species may avoid roads even in the absence of hunting pressure along them; alternatively, they may associate roads with hunting and avoid them, but not distinguish different forest areas as threatened by hunting. Elephants, on the other hand, were negatively affected by hunting and roads, but were attracted to villages (probably to raid crops). More research is necessary to determine the types and intensity of human disturbance that affect different species.

### Assessing Species Responses to Logging

Our models of species presence and abundance often differed with the variables retained—and sometimes, even the direction and effect size of the important variables differed—which suggests that the ecological factors determining species presence may differ from those determining species abundance. By decoupling the processes that determine the presence and abundance of a species, a fuller understanding of how logging affects mammal populations can be gained. Importantly this demonstrates that simple surveys of animal presence (e.g., for rapid assessment) may not give a full picture of a species response to disturbance and may misinform management.

To our knowledge we are the first to examine response curves of tropical forest mammals in relation to time since logging and other explanatory variables. Although other studies have monitored animal populations for many years after logging, they typically treated data in

a discrete manner: logging affects abundance positively, negatively, or not at all. The management of logging concessions for animals depends on understanding species responses to the direct and indirect effects of logging, especially because species abundance can change over time with forest recovery so that management decisions based on present abundances may be wrong for the trajectory of the animal population.

### Management Recommendations

Our results provide initial evidence that managed production forests can extend, but not replace, the conservation estate. The logging concessions in our study encompassed a large area, were varied in habitat and logging history, had only been logged once, included relatively large areas that were unlogged and mostly free of hunting pressure, and were adjacent to a national park. These conditions are unlikely to be met in most tropical logging concessions and will be altered as the second rotation of logging occurs and human population grows. Nonetheless, several management steps can be taken to promote wildlife conservation in production forests: (1) establish hunting and no-hunting zones in collaboration with communities and enforce hunting laws, (2) establish no-logging and no-hunting zones around important or rare wildlife habitat (e.g., natural forest clearings), (3) close all inactive logging roads to traffic and limit the use of active roads to company vehicles and personnel, (4) organize movements of logging vehicles to minimize vehicle activity on roads, (5) plan logging rotations at long time intervals (e.g., 30 years) that are spatially separated to allow sufficient time for vertebrate and plant population recovery and creation of diverse habitats within a single concession, (6) implement reduced-impact logging techniques, and (7) establish monitoring protocols to identify and mitigate threats to biodiversity. Our results demonstrate that logged forest may contribute to the conservation of large tropical mammals, but its application to other forests will likely depend on careful monitoring and management.

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## Supporting Information

Map of study site in northern Republic of Congo (Appendix S1), GAM model equation and details (Appendix S2), and mean species abundances as a function of explanatory variables (Appendix S3) are available as part of the on-line article. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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