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Discriminating between village and commercial hunting of apes

Hjalmar S. Kuehl [a,*], Christian Nzeingui [b], Stephane Le Duc Yeno [b], Bas Huijbregts [b]
Christophe Boesch [a], Peter D. Walsh [a]

[a] Max-Planck-Institute for Evolutionary Anthropology, Department of Primatology, Deutscher Platz 6, 04103 Leipzig, Germany
[b] World Wide Fund for Nature, WWF Gamba, P.O. Box 1944, Libreville, Gabon

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ABSTRACT

Hunting is the major driver of large mammal decline in Central African forests. In slowly reproducing species even low hunting pressure leaves spatial gradients with wildlife density increasing with distance from transport routes and human settlements. Park management can use this pattern formation to identify sources of threats, but also to discriminate between different threat scenarios, such as the impact of subsistence vs. commercial hunting. We conducted an ape survey in the mountainous Moukalaba Doudou National Park, Gabon, to evaluate whether potential population gradients would emanate from the three human population centers in the region or the villages surrounding the park. Using generalized linear modeling we found hill slope as a good predictor of ape nest occurrence probability and the distance to human population centers a better predictor of ape nest density and ape nest group size than distance to villages. In fact ape nest density was three times lower at the park borders close to the human population centers than in the park's interior. The results indicate that Moukalaba's ape population is more impacted by commercial than subsistence hunting and suggest that park management should focus conservation efforts on the human population centers. We conclude that in particular for slowly reproducing species geographic information on wildlife population gradients are of additional value for guiding protected area management. The hunting impact on those species might be easily underestimated, if derived only from market surveys or transport route controls, where they are only rarely found.

1. Introduction

The large mammals of Central Africa's forests are in a state of rapid decline (Huijbregts et al., 2003; Walsh et al., 2003; Bermejo et al., 2006; Blake et al., 2007). Conservation funds are scarce so that stemming this decline will require focusing resources on programs that most directly address the major threats (Ferraro and Pattanayak, 2006). The leading threat is hunting (Oates, 1999; Ammann, 2001; Wilkie and Carpenter, 1999; Wilkie, 2001). However, the nature of hunting varies from site to site (Fa et al., 2005). At some sites, hunting is a subsistence activity that is conducted by local people and emanates from traditional villages of long tenure (e.g. Muchaal and Ngandjui, 1999). At other sites, hunting is primarily a commercial activity that satisfies demand in distant urban markets and is often conducted by hunters who are not local inhabitants (e.g. Wilkie and Carpenter, 1999; Ammann, 2001; Fa et al., 2002; Edderai and Dame, 2006).

The distinctions between subsistence and commercial hunting and local and non-local hunters are critical for conservationists because they determine which conservation strategies will be most effective at conserving large mammals (e.g. Pullin and Knight, 2001, 2003; Sutherland et al., 2004; Nichols and Williams, 2006). For instance, programs designed to provide local villagers with alternative livelihoods, protein, or value for wildlife (e.g. through tourism) may be very effective if subsistence hunting by locals is the major threat. However, they may not be effective, if the major threat is commercial hunting by outsiders. Likewise, control points along transport routes (roads, rails, rivers, or airports) or inspections at markets may be effective at reducing commercial hunting but not very productive as methods for controlling subsistence hunting.

Although these distinctions indicate what the appropriate strategy might be, shortcomings in current methods for monitoring hunting can make it difficult to quantify how much impact each type of hunting is having on large mammal populations at a given site. For example, interviews with hunters may allow the monitoring of rates of individual hunter offtake (e.g. Cowlishaw et al., 2005). However, some hunters may resist or evade participation in such monitoring efforts: particularly non-local and/or commercial hunters. Even local, subsistence hunters may be hesitant to re-

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* Corresponding author. Tel.: +49 (0) 341 3550 236; fax: +49 (0) 341 3550 299.
E-mail addresses: kuehl@eva.mpg.de (H.S. Kuehl), leducyeno@yahoo.fr (S.L.D. Yeno), huijbregts_bas@hotmail.com (B. Huijbregts), boesch@eva.mpg.de (C. Boesch), walsh@eva.mpg.de (P.D. Walsh).

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port offtake of protected species such as apes. For similar reasons, protected species may tend to be undercounted in market surveys (e.g. Thibauldt and Blaney, 2003) .

A further problem is that offtake does not equal impact. The population response to hunting offtake is a complicated function of the life history, social structure, abundance and local ecology of a given species (e.g. Refisch and Koné, 2006). Thus, although it is safe to presume that the resiliency to offtake should tend to decrease with longevity, it is very difficult to predict exactly how big a problem a given level of offtake is. Is one chimpanzee per hunter per year a little or a lot?

Here we explore an alternative approach to discriminate between the population impacts of subsistence vs. commercial hunting that exploits the tendency for hunting to generate gradients in large mammal density. The most well known instance of gradient creation may be the tendency for the density of species such as elephants and apes to increase with increasing distance from points of hunting access (Blom et al., 2005; Laurance et al., 2006; Blake et al., 2007). However, large mammal density has also been shown to increase with distance to villages (e.g. Muchaal and Ngandjui, 1999) and human population centers (Wilkie and Carpenter, 1999; Walsh et al., 2003). Here we propose that the scale and orientation of such gradients provides valuable information about the nature of hunting impact. If subsistence hunting has had a strong impact on large mammal populations, then distance from villages should be a good predictor of large mammal density. If commercial hunting is a problem, then distance to human population centers should be a good predictor.

To test this hypothesis we used data from transect surveys of great apes conducted in the Moukalaba Doudou National Park in Southwestern Gabon. This Park holds one of the largest remaining populations of sympatric chimpanzees and gorillas (Tutin et al., 2005). Apes are not a particular focus of local bush meat consumption in the area and are rarely seen in local markets or at road control points (Thibauldt and Blaney, 2003). However, apes have very long generation times, making them highly vulnerable to even very low hunting pressure (Kormos et al., 2004; Rizkalla et al., 2003). Therefore, we used generalized linear modeling (GLM) methods to look for evidence of population impact from hunting. In particular, we evaluated whether ape population density gradients emanated from local villages bordering the Park and from the human population centers lying at a greater distance from the Park. To control for other factors that might generate ape population gradients, we also included a set of environmental variables (e.g. topography and vegetation type) in our GLM's.

2. Methods

2.1. Study area

Our study area, Moukalaba Doudou National Park, is situated in southwestern Gabon. The Park stretches north from the Atlantic coast (Fig. 1) and is part of the 12,000 km^2 Gamba-Complex of protected areas (Thibault et al., 2001). The park comprises about 4470 km^2 dominated by the Doudou mountains, with peaks up to 700 m. Large regions of the park interior are extremely steep and difficult to access. Vegetation cover is dominated by secondary tropical rainforest. The Nyanga savannahs and marshland cover a smaller area in the south of the Park. Several dozen villages are in close vicinity to the park. The towns (hereby referred to as human population centers, including the many settlements in the towns' vicinity) of Gamba (~10,000 people), Tchibanga (~18,000 people), and Mandji (~10,000 people) are respectively situated about 30 km southwest, 30 km southeast, and 20 km north of the Park. The Park boundary is formed by the rivers Bongo on the west and Moukalaba on the south east. These rivers and the Nyanga River in the south provide access to peripheral areas of the Park. Foot access to some areas of the interior is provided by former logging roads that are now impassable to vehicles.

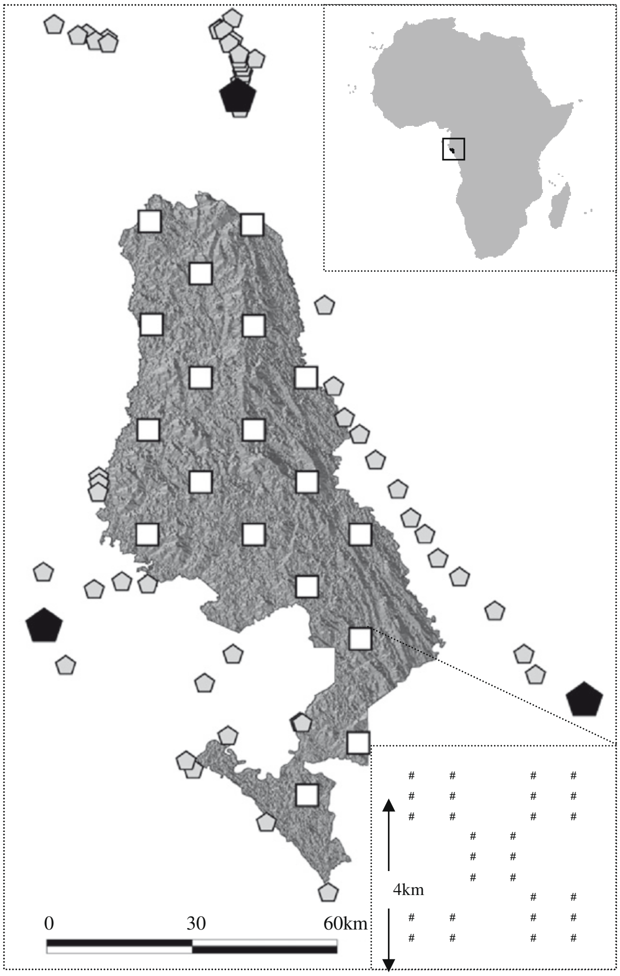

Fig. 1. Map of Moukalaba Doudou National Park, villages (grey rhombs), and human population centers (black rhombs). The survey design is represented schematically (white squares). Each square contained a total of 30 point transects (inset).

2.2. Field methods

From April 2004 to July 2005, we sampled ape sleeping nest densities using transects, the standard method for surveying apes (e.g. Morgan et al., 2006). Due to inaccessibility, we excluded the papyrus swamps in the south from the survey, which reduced the survey area by 296–4176 km^2. The extremely steep terrain in the interior of the Park would have made it impossible to complete a large proportion of sampling units, if we had employed the sampling method most commonly used in ape studies, line transects (e.g. Plumptre, 2000; Morgan et al., 2006). A survey conducted previously using recces and lines transects, did not cover the entire park, but mainly the periphery. We therefore used instead the point transect methodology (Buckland et al., 2001), which we slightly modified. We did not sample transects located in very steep terrain, where it was to dangerous to work, or which fell into swamps or rivers. Each point transect had a diameter of 100 m and was sampled with decreasing intensity from the center towards the edge. At each transect, five observers walked in concentric circles recording ape nests with an integrated GPS and data logging device (Cybertracker, Bellville, South Africa). The observers made two circuits of the transect center point, the first with 3 m between observers and the second with 10 m between observers.

Travel is extremely demanding in large parts of the Park, with travel speed often less than 0.5 km/h. With an equally spaced survey design, about three quarter of total time would have been allocated to travel. Therefore, we used a hierarchically clustered survey design (Fig. 1), which provided a much better travel to sampling time ratio. We grouped six transects in blocks of one by one km, and combined five of these blocks into larger units of 30 point transects. The design included 18 of these larger units: with 540 point transects in total. Consequently our sampling locations were not independent (see Section 3).

3. Analytical methods

3.1. Predictor variables

We used two groups of variables: environmental predictors and distance-based proxies for hunting accessibility. The environmental predictors included both topographic variables (altitude and slope) as well as a metric of vegetation type. The topographic variables altitude and slope we extracted from the 90 m resolution SRTM digital elevation model (downloadable from Global Landcover Facility, http://glcf.umiacs.umd.edu/data/). We used vegetation information derived from a classification based on Landsat TM, radar and aerial imagery (Ministere des Eaux et Forêts et du Reboisement, Tecsult International, Quebec Canada; provided by WWF Gamba). The vegetation classification distinguished four broad vegetation types: secondary forest, temporary and permanently inundated forest, inaccessible forest and Savanna/gallery forest. We assigned this vegetation information to each transect based on GPS location.

As proxies for hunting intensity we used both the Euclidian distance to villages and human population centers (Gamba, Tchibanga, and Mandji) and a cost–weight distance that accounted for variation in travel speed. The Euclidian distances measured (in ArcView v.3.2) a straight line from each sample point to the nearest village or market town.

We used the cost weight distances to account for different travel speeds on roads and rivers as well as on forest trails, using empirical observations to estimate travel speed for each travel mode. For foot travel within the Park, we also accounted for the effect of topography on travel speed by deriving a "friction" value (Y, IDRISI 32, Clark Labs),

$$Y = (0.031 * \sqrt{\text{slope}}) - 0.025 * \text{slope} + 1.$$

This approach provides "grid cell equivalents" (a reference value of one for cells with zero slope, and a multiple of that for cells with steeper slope). We then used the IDRISI 32 software package to derive a least cost path from each sampling point to the nearest village or market town.

3.2. Covariate model

Our approach to covariate modeling was guided by the fact that in ape surveys the number of nests detected per transect tends to show a highly skewed distribution. Many transects do not have any nests; a very few have up to several dozen. To deal with overdispersion we used two analytical approaches. First, we used logistic regression (McCullagh and Nelder, 1989) to estimate the probability of detecting at least one nest on transect k

$$P(Y_k) = \frac{1}{1 + \exp(-(b_0 + \sum_{i=1}^{i=q} b_i x_i + b_{\text{ac}}\text{ac}_k)},$$

where the b's are constants and x's are the covariates. The variable *ac* is an autocorrelation term that accounts for the spatial non-independence of sampling locations. We calculated the autocorrelation term for each sample site following Lichstein et al., (2002)

$$\text{ac}_k = \sum\nolimits_{j \neq k} \frac{1}{w_{jk}} (Y_j - \mu_j),$$

where w_{jk} is the distance between transect k and transect j, Y_j is the observed value at transect j and μ_j is the expected value at location j based on the covariate prediction alone.

As a second approach we use a GLM with the number of nests (n) as the response (Hedley and Buckland, 2004), a natural log link, and quasipoisson error distribution, which models for overdispersion (McCullagh and Nelder 1989),

$$n_k = \exp\{\ln(\pi r_i^2) + b_0 + \sum\nolimits_{i=1}^{i=q} b_i x_i + b_{\text{ac}}\text{ac}_k\}.$$

Where $\ln(\pi r^2)$ is an offset term for the effective area surveyed.

To evaluate whether ape population gradients were associated with changes in mean nest group size (rather than just group density), we also conducted a GLM with mean nest group size as the response variable. However, as group size is a continuous response, we used a Gamma error distribution (link = log).

For each response variable (presence–absence, nest count, nest group size) we evaluated models including all possible combinations of effects, including a baseline model with only a constant nest density. However, for the sake of rhetorical simplicity we present results from only six models below: the baseline model, a model with an autocorrelation term but no covariate predictors, and models that included the autocorrelation term and either Euclidian distance to village, cost weight distance to villages, Euclidean distance to human population centers, or cost weight distance to human population centers.

For the GLM's with binomial and gamma error distributions (presence–absence and nest group size), we used maximum-likelihood methods to estimate parameter values and AIC (Akaike's information criterion) to select models (Burnham and Anderson, 2002). For the GLM with quasi-Poisson error distribution we used ANOVA for model selection (Faraway, 2006). For assessment of fit,

Table 1

Logistic regression results with nest absence/presence as response variable: listed are five of the models evaluated, and a null model with no effect, the number of parameters in each model, AIC, and the parameter estimates for the constant (const) and the variables: Ac = autocorrelation term; alt = altitude [m], slope = hill slope [deg]; veg = vegetation; vil = distance to villages (dist – vil = Euclidian distance [m]; cw – vil = cost weight distance [dimensionless]); pc = human population center (dist – pc = Euclidian distance [m]; cw – pc = cost weight distance [dimensionless]). The parameters listed for vegetation are for the classes Savanna, inundated forest, inaccessible forest; reference was the class secondary forest.

Model	#Par	AIC	Const	Ac	Alt	Slope	Veg	Vil	Pc
Ac	1	585.2	0.503	2.303					
Ac + alt + slope + veg	7	584.0	0.353	0.390	−0.0019	0.067	1.059/−0.028/0.032		
Ac + alt + slope + veg + dist – vil	8	585.4	0.465	0.352	−0.0019	0.067	1.030/0.005/0.049	−5.7E−05	
Ac + alt + slope + veg + cw – vil	8	585.5	0.334	0.381	−0.0019	0.067	1.064/−0.034/0.029	9.2E−05	
Ac + alt + slope + veg + dist – pc	8	585.6	0.352	0.389	−0.0019	0.067	1.059/−0.027/0.032		1.87E−08
Ac + alt + slope + veg + cw – pc	8	585.4	0.236	0.421	−0.0020	0.068	1.05/−0.043/0.007		2.9E−04

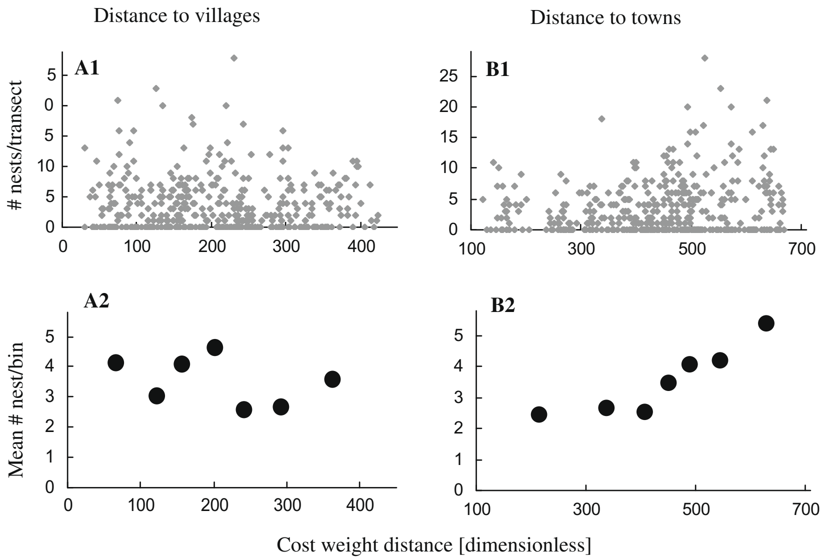

Fig. 2. Scatter plot of number of ape nests per transect plotted against cost weight distance [dimensionless] to villages (A1, left) and human population centers (B1, right); $n = 439$; in A2 and B2, data represented as equally sized bins ($n = 7$; bin size = 64).

we used the standard diagnostic plots (Residuals, Leverage and influence, QQ plots, Cook's distance) to investigate conformity to model assumptions (Faraway, 2006).

3.3. Surface prediction

To predict surfaces of ape nest occurrence, nest density and nest group size for the entire park, we used the best fitting models for each response variable. We divided the park into 0.5 × 0.5 km (0.25 km^2) grid cells, for which we extracted covariate information. We then predicted values for each cell. Statistical analyses were done in R (R Development Core Team, 2005) and maps were created in ArcView v. 3.2.

4. Results

We sampled 439 of the 540 point transects contained in the original design. Hundred and one transects were located either in inundated or steep, inaccessible terrain, and were not sampled. We encountered a total of 1543 ape nests in 344 groups, with mean ape nest group size of 4.5 ± 3.4 (SD).

4.1. Presence/absence of ape nests

Logistic regression revealed no large scale gradients in ape nest occurrence probability. Ape nest occurrence was neither influenced by distance to villages, nor distance to human population centers (Table 1). The probability of encountering at least one nest

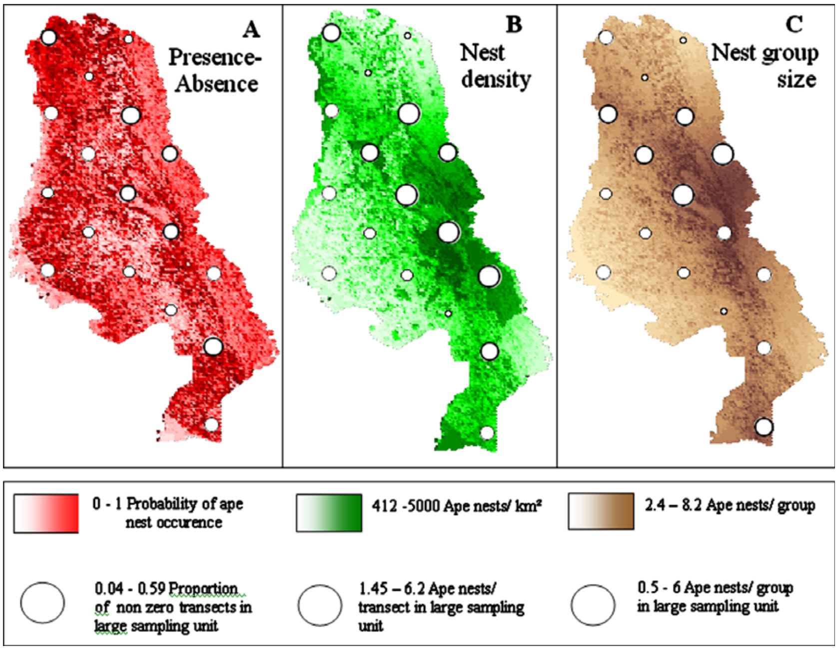

Fig. 3. Predicted surfaces of ape nest occurrence probability (A), ape nest density (B) and ape nest group size (C), based on the best fitting model, respectively. For the prediction we excluded the inaccessible southern part of the park with the Nyanga swamps.

Table 2

Glm results for models with nest encounter rate as dependent variable: listed are the eight models evaluated, and a null model with no effect, the number of parameters in each model (constant included), the residual deviance (res.dev), deviance (dev), residual degrees of freedom (res.df), degrees of freedom (df), *F*-statistics (*F*), *p*-value (*p*), and the parameter estimates for the constant (const) and the variables: Ac = autocorrelation term; alt = altitude [m], slope = hill slope [deg]; veg = vegetation; vil = distance to villages (dist – vil = Euclidian distance [m]; cw – vil = cost weight distance [dimensionless]); pc = human population center (dist – pc = Euclidian distance [m]; cw – pc = cost weight distance [dimensionless]). The parameters listed for vegetation are for the classes Savanna, inundated forest, inaccessible forest; reference was the class secondary forest.

Model	#par	res.dev	dev	res.df	df	*F*	*p*	const	ac	alt	slope	veg	vil	pc
Ac	1	2265.45	47.24	437	5	1.6814	0.1377	−3.31	0.285					
Ac + alt + slope + veg	7	2218.22	26.85	432	3	1.5994	0.1904	−3.65	0.237	−4.8E−04	0.028	0.466/0.536/−0.228		
Ac + alt + slope + veg + dist – vil	8	2214.77	3.45	431	1	0.6181	0.4322	−3.50	0.227	−5.1E−04	0.028	0.439/0.574/−2.11	−1.29E−05	
Ac + alt + slope + veg + cw – vil	8	2216.12	2.09	431	1	0.3739	0.5412	−4.55	0.105	2.6E−05	0.034	0.458/0.475/−0.338	−7.8E−04	
Ac + alt + slope + veg + dist – pc	8	2184.75	33.47	431	1	6.2137	0.0131	−3.42	0.217	4.9E−04	0.028	0.426/0.594/−0.203		2.35E−05
Ac + alt + slope + veg + cw – pc	8	2172.71	45.51	431	1	8.6340	0.0035	−4.64	0.154	−2.9E−04	0.035	0.423/0.439/−0.357		2.13E−03

on a sampling unit was relatively homogenous throughout the park with $P(Y_k) = 0.62$. In contrast, ape nest occurrence probability showed a strong positive relationship with hill slope (Fig. 3a, Table 1). Neither the vegetation type nor altitude was a good predictor of nest presence.

4.2. Ape nest density

In sharp contrast to the absence of large scale gradients in ape nest occurrence probability, ape nest density strongly increased with increasing distance from the human population centers (Table 2, Fig. 2b). However, we found no effect of distance to villages on the border of the Park (Fig. 2a). The cost weight distance model, accounting for differences in travel time, fit slightly better than the Euclidian distance model, but the improvement was not large. Ape nest density increased by a factor of two from the border of the park to the interior. Ape nest density was highest along the ridgeline of the Doudou mountains in the central part of the park, and in the east (Fig. 3b).

4.3. Ape nest group size

Ape nest group size also varied with both local topography (hill slope) and distance to the major human population centers (Table 3). Similar to ape nest density, ape nest group size did not vary with increasing distance to villages. Ape nest group size in the interior of the park was about twice as high as group size at the border of the park in close proximity to one of the towns (Fig. 3c).

5. Discussion

Market surveys have long suggested high rates of bushmeat offtake from Moukalaba Doudou National Park and surrounding protected areas (Thibauldt and Blaney, 2003). However, ape meat rarely appears in surveys of local bushmeat markets. Thus, one might conclude from the market data that commercial hunting was not a serious threat to apes. However, our survey results imply that commercial hunting emanating from major market towns has induced a strong gradient in ape density in the park. The lack of a detectable ape density gradient around traditional villages bordering the Park not only suggests that subsistence hunting is not the primary cause of ape offtake but that the inhabitants of traditional villages are not the primary agents of commercial hunting. The observation that hill slope was correlated with ape nest encounter rate is also consistent with hunting as a major determinant of ape distribution, as steep hills are known to provide gorillas refuge from hunting in areas such as the Cross River region of Nigeria and Cameroon (Oates et al., 2003; Bergl and Vigilant, 2007, but see also e.g. Morgan et al., 2003 for Ebo forest, Cameroon). The lack of an effect of vegetation type on nest encounter rate also suggests that the observed gradients in ape density were not induced by large scale trends in vegetation cover, although our relatively simple approach to representing vegetation effects may not have quantified the pertinent aspects of vegetation composition or structure adequately.

It is not clear whether the observed scarcity of ape meat in local markets simply reflects the low densities and reproductive rates of apes or is an indication of the tendency for bushmeat vendors to conceal the meat of apes and other protected species. Whatever the case, our results suggest that the kind of surveys reported here can be a valuable complement to methods such as market surveys and hunter interviews in assessing not just the impact of hunting on apes but also the economic drivers of hunting. And the latter information is critical in targeting conservation efforts. Both the general implica-

Table 3

GLM results of model with nest group size as response variable: listed are the eight models evaluated, and a null model with no effect, the number of parameters in each model, AIC, and the parameter estimates for the constant (const) and the variables: Ac = autocorrelation term; alt = altitude [m], slope = hill slope [deg]; veg = vegetation; vil = distance to villages (dist – vil = Euclidian distance [m]; cw – vil = cost weight distance [dimensionless]); pc = human population center (dist – pc = Euclidian distance [m]; cw – pc = cost weight distance [dimensionless]). The parameters listed for vegetation are for the classes Savanna, inundated forest, inaccessible forest; reference was the class secondary forest.

Model	#Par	AIC	Const	Ac	Alt	Slope	Veg	Vil	Town
Ac	2	1322.1	1.517	0.189					
Ac + alt + slope + veg	7	1326.5	1.336	0.200	0.0004	0.014	0.027/–0.06/–0.122		
Ac + alt + slope + veg + dist – vil	8	1328.4	1.386	0.199	0.0004	0.014	0.016/–0.051/–0.188	–2.7E–06	
Ac + alt + slope + veg + cw – vil	8	1328.3	1.393	0.199	0.0004	0.014	0.016/–0.048/–0.117	2.8E–04	
Ac + alt + slope + veg + dist – pc	8	1321.6	0.669	0.104	–0.0004	0.017	–0.04/–0.144/–0.160		1.7E–05
Ac + alt + slope + veg + cw – pc	8	1320.0	0.777	0.076	–0.0002	0.018	0.04/–0.13/–0.144		0.001

tion of commercial hunting and the specific effect of hunting accessibility suggest that transport interdiction may be an effective strategy for fighting ape decline in Moukalaba Doudou. Checkpoints on roads and rivers not only have the potential to apprehend illegal hunters, they induce an additional travel cost for those seeking to evade detection. And if our results show anything, they show that travel costs are a major determinant of hunting risk to apes.

The landscape history of western equatorial Africa suggests to us that similar approaches to both monitoring and conservation may be productive at other sites in the region. Moukalaba Doudou is only one of a series of large blocks of habitat from which villages were forcibly relocated during the early part of the last century. In following years economic migration to major cities further eroded the density of people around these large habitat blocks. It is only in the last few decades that commercial resource extraction enterprises (oil exploitation in coastal areas such as Gamba, logging and mining in the interior) have drawn migrants to new towns near the large habitat blocks. These new towns provide a market of salaried employees to buy bushmeat while neighboring large blocks of habitat have little or no traditional land tenure that might exclude newcomers from hunting access. For example, on the 80 km long western border of Moukalaba Doudou National Park there is only one small village with about 20 inhabitants. Thus, even if programs targeted at preventing bushmeat offtake by local villagers worked perfectly, they might have little impact on the hunting of apes and other species. A similar situation prevails at many other remaining large populations of gorillas and chimpanzees, including major strongholds such as Odzala and Nouabale-Ndoki National Parks in Republic of Congo.

We certainly do not advocate the total abandonment of conservation programs targeted at local villagers. These have clear benefits and will remain an important part of the conservation puzzle. Rather, we are simply saying that getting the mix of conservation activities right at a given site requires an objective assessment of the nature of threats at that site. Applied in combination with other methods, the approach presented here has the potential not just to detect the impact of commercial hunting but also, through repeated monitoring, to evaluate the success of conservation efforts in terms of the time evolution of density gradients in parks. However, given the very low reproductive rate of apes, this might be easier for more rapidly reproducing species, e.g. monkeys, duiker.

Of course, the survey approach applied here is not perfect. For instance, the extremely low rates of travel attainable in the Doudou Mountains moved us to use a clustered survey design in order to improve the travel to sampling time ratio. Unfortunately, this produced both less uniform spatial coverage and a smaller of truly independent samples than might have been achieved with an equally-spaced design. We feel that our use of an autocorrelation term adequately addressed the issue of sample non-independence. However, we are aware that more fine grained spatial coverage might have given us greater statistical power for detecting (weak) hunting gradients emanating from villages. The issue of how to design surveys so as to optimize the balance between travel costs and spatial resolution deserves more research attention in the future.

Another problem we were aware of from the outset was that ape transect nest counts tend to be highly skewed with many transects having no nests and a few several dozen. This skew reflects the structuring of apes into social groups, aggregated patterns of ape habitat use by social groups, and the relatively low density of apes. It complicates trend estimation because the error models typically used in the analysis of count data tend to assign very low probabilities to events falling far from the mean. Consequently, occasional large nest counts tend to produce very large confidence intervals and low statistical power: a serious issue given the sample size problems induced by high travel costs. We attempted to solve this problem by using a variety of different response models, each of which was sensitive to a different property of the data. This appeared to work well with our nest count and group size models. However, the failure of our logistic regression models to detect any spatial trends illustrates that caution must be taken in interpreting results when skew is strong. Further work is clearly necessary before we asymptote on efficient methods for analyzing ape nest count data. An interim solution is simply to maximize sample size and, thereby, improve precision. This, in fact, was one of the rationales behind our choice of point transects and a clustered sampling design: which allowed more sample replicates.

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