

The spatial structure of hunter access determines the local abundance of forest elephants (*Loxodonta africana cyclotis*)

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Abstract. In many previously remote regions in the world, increasing and often unregulated access is leading to dramatic increases in hunting pressure and declines in the densities of prey species, sometimes to the point of local extinction. Not surprisingly, numerous studies have found a correlation between the distance to the closest access point and prey densities. Here we hypothesized that, for many wide-ranging species, local abundances are reduced by hunting associated with multiple access points as opposed to just the closest access points. We also hypothesized that the distribution of hunter access determines both patterns of occupancy and abundance in occupied areas and that these two patterns (occupancy and abundance) respond to access at different spatial scales. Using data on the distribution of abundances of African forest elephant (*Loxodonta africana cyclotis*) in and around five national parks in Central Africa, we tested these hypotheses using a model comparison framework.

We found that models including an index based on the distance to multiple roads outperformed models including other access-based covariates, including a model based on distance to the closest road only. We also found that models that allowed us to model occupancy and abundance separately outperformed simpler models. Occupancy responds to access at the same scale as previous estimates of average maximum displacement in the subspecies, while the scale of the response of abundance is more ambiguous, but appears to be greater. Lastly, we show that incorporating indices based on multiple access points and modeling abundance and occupancy has important practical consequences for our understanding of overall regional abundances and the distribution of abundances within regions.

Key words: access; African forest elephant; hunting; *Loxodonta africana cyclotis*; range collapse; roads; wide-ranging mammals.

INTRODUCTION

Species-based conservation relies on estimates of the distribution and abundance of the target species to develop and prioritize management responses (Caughley and Gunn 1996, Wikramanayake et al. 1998, Sanderson et al. 2002a, b, Blake and Hedges 2004, Sanderson 2006). These estimates are often derived from survey data and influenced by assumptions about the spatial structure of populations of the targeted species and the distribution and intensity of threats within and around the survey area. Hunting has been identified as a key

threat for many species of conservation concern (Wilcove et al. 1998, Li and Wilcove 2005). The distribution of hunting pressure in remote forested areas is largely determined by the location of access points. Points of access into otherwise remote areas are generally found near settlements, rivers, and roads (Barnes et al. 1997, Wilkie et al. 2000, Laurance et al. 2006, Blake et al. 2007). Not surprisingly, studies have established that the probability of occurrence and the relative densities of exploited species increase with distance from access points (Barnes et al. 1991, Peres and Lake 2003, Blom et al. 2005, Blake et al. 2007).

The character of this relationship (in terms of the distance at which densities reach undisturbed levels and the degree to which densities are lowered in the most affected areas) varies greatly between different animal species (Peres and Lake 2003). Clearly, differences in human hunting preferences, intensity, and efficiency can explain some of this among species variation; however,

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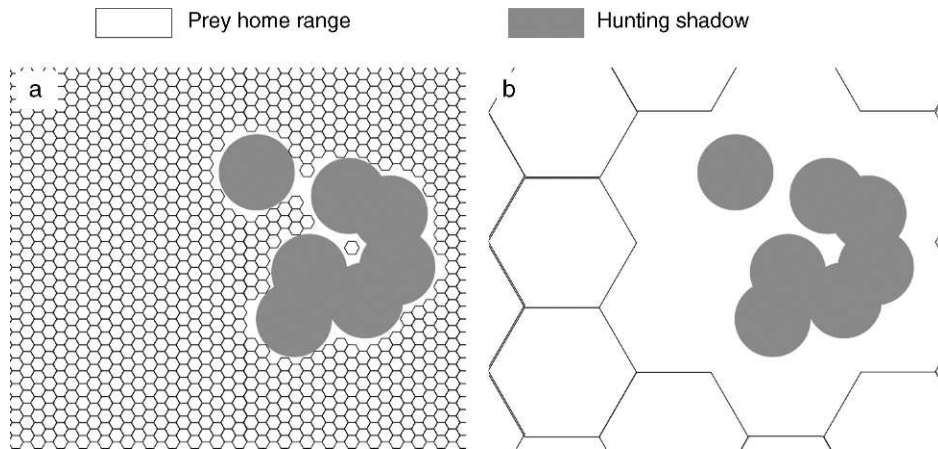


FIG. 1. Conceptual model of the interaction between the distribution of a threat (in this case the hunting shadow around access points) and the spatial population structure of a prey species. Hexagons illustrate the scale of home ranges or local populations of a given target species, while the shaded areas around the access points represent the extent of the direct impact of the access points (i.e., the extent of the hunting shadow). The boundaries of hexagons overlapping the hunting shadow were left blank to illustrate the difference in the extent of the impact of a threat on (a) a restricted and (b) a wide-ranging prey species. We expect that distance to the closest access point will be an adequate proxy for the impact of hunting when access points are isolated or when prey species restrict their movements to areas that are smaller than the extent of the hunting shadow around a single access point.

aspects of the spatial structure of prey populations may also play an important role in determining the distribution of abundances in hunted landscapes. One concept of spatial population theory, source–sink dynamics (Pulliam 1988), has already been applied in the context of landscapes with patchy distributions of hunting pressure to explain why populations of exploited species persist in hunted areas when levels of hunting are locally unsustainable (Mace and Waller 1988, Novaro et al. 2000, 2005, Naranjo and Bodmer 2007, Robinson et al. 2008). In these landscapes, it is believed that migration from non- or lightly hunted areas to hunted areas compensates for the increased mortality in hunted areas.

While source–sink theory has been invoked to explain the resulting differences in mean densities between hunted and neighboring areas, this theory ignores the spatial details of dispersal (focusing only on net immigration) and daily movements in determining finer scale distributions of densities. That is, source–sink models assume a series of discrete prey populations in which individuals are exposed to homogeneous levels of hunting pressure and among which there is no exchange of individuals except in terms of permanent migration. Furthermore, many studies assume that the extents of these discrete populations are determined solely on the basis of the distribution of hunting (a human-centered perspective) without reference to the biology of the prey species.

These assumptions are rarely met in the real world, where local populations are rarely discrete, individuals (not populations) are exposed to different environmental conditions, and the movements of individuals (not the distribution of a threat such as hunting) determine the extent of local populations. One implication of the failure of these assumptions is that even if hunting

pressure (or some other threatening process) is distributed evenly in two or more different areas with well-defined borders, the impacts on densities are not expected to be evenly distributed within the different areas. The impacts are not expected to be evenly distributed because population processes will occur across the borders and some individuals will move between patches as part of their normal ranging behavior.

The importance of individual movement processes and local population processes in determining the final distribution of densities will vary depending on how the spatial extents of these two processes compare to the spatial extent of hunting around an access point (i.e., the hunting shadow). For many species, the spatial extent of both the local populations and individual home ranges will be less than the extent of the hunting shadow (Fig. 1a). For these species, interspecific variation in the behavioral responses to lowered densities (e.g., territory or home range expansion), dispersal ability, and growth rate of the source populations can help explain disparities between taxa in the separation from the closest access point required for densities to return to non-hunted levels. For some species, however, the spatial extent of individual home ranges and local populations will be greater than the extent of the hunting shadow (Fig. 1b), and as a result the impact on densities may extend far beyond the extent of the hunting shadow. For example, individuals within home ranges that overlap a hunted area will have a higher likelihood of being killed than those have no overlap, even if they spend much of their time in areas that are not hunted. The effect of hunting on densities could extend even further if neighboring individuals respond to the loss of individuals from hunting by increasing

their territory or home range size to occupy vacant areas.

Furthermore, we would expect that if the spatial extents of individual home ranges and local populations are sufficiently large (relative to the spatial extent of the hunting shadow) and there are multiple sources of threats (i.e., multiple hunting access points), then densities at a given location may be a function of the location and distance to multiple threats, not just to the closest one. While this expectation may seem intuitive, most analyses of the impact of hunting on prey densities have assumed that only the closest access points matter. The dependence of local abundances on the spatial structure of access points could arise through two pathways, which are not mutually exclusive. First, individuals whose home ranges previously overlapped with the hunting shadow are more likely to have died or to have shifted their home range into other areas leading to a decreased probability of any individuals being present at the spatial scale of home ranges and leading to a home-range-scale response (HRSR). At larger spatial scales, areas around hunting shadows will act as sink habitat, and increases in the proportion of the ratio of sink to source habitat may eventually lead to lower densities, even in areas that are separated from hunting zone by more than one home range. This local population-scale response (LPSR) should operate at spatial scales larger than the HRSR and should affect densities in occupied areas.

If both the LPSR and the HRSR are operating then we would expect that, at the scale of individual home ranges, increasing overlap with threatening processes will increase the likelihood that an area will be unoccupied, while at the scale of the local population, the amount of overlap with threatening processes will determine the aggregated mortality and thus the average density of the local population. One way to test this two-process hypothesis is to model both processes using two separate generalized linear models. Presence (interpreted here as some non-negligible probability of use by individuals of a species) at each location could be modeled by linking predictors to the binomial statistical distribution through the logit link (i.e., as in logistic regression), while abundances in occupied locations could be modeled by linking a separate set of predictors to the statistical distribution for count data (Poisson or negative binomial) via the logarithm link. Modeling both occupancy (presence) and abundance is useful when the factors determining species presence are distinct from the factors that determine density in occupied areas (Cunningham and Lindenmayer 2005). In particular, when the two processes responsible for presence and densities operate on different spatial or temporal scales (Wenger and Freeman 2008).

One potential pitfall of modeling presence and abundance in separate sets of models is that all zeros are included in the occupancy model and excluded from the count (abundance) model. This is problematic

because we would expect some zeros in a count data set with a small mean, and removal of these zeros in the count model can bias the results of both models (Warton 2005). Fortunately, we can overcome this problem, while still modeling both components of the two-process model, by fitting the occupancy and count models simultaneously using models based on zero-inflated count distributions (specifically the zero-inflated negative binomial distribution). This statistical model is consistent with the general view that ranges are structured hierarchically and that range collapse can occur through losses at the level of individual home ranges as well as declines in local populations (Gaston 2003). A key distinction apparent in both the hierarchical conceptual model and this statistical model is that absences (zeros) can arise either because an area is locally unsuitable (high probability of zero in the occupancy portion of the model) or because an area is suitable but the neighborhood of the area is unsuitable (leading to a low predicted density in the count portion with a high likelihood of a zero count). Since the probability of zero in a zero-inflated distribution never actually reaches 1 (as a result of its being linked through the logistic function), this model also allows for the possibility of detection of dispersers in unsuitable areas bordering suitable areas, another key issue in range structure, particularly along range edges (Gaston 2003). This issue is particularly important for wide-ranging species that are more likely to travel long distances outside suitable areas because of their greater mobility.

The hypothesis that the distributions and local abundances of species with larger home ranges will be affected by the spatial distribution of hunting, or more generally, threats, through either of the two response pathways is largely untested with a few key exceptions. For example, some studies have applied similar logic to the HRSR to explain why species with large home ranges are more vulnerable to local extinction in small protected areas due to edge effects (Woodroffe and Ginsberg 1998, 2000). More recently, Frair et al. (2008) determined that home range occupancy of elk in Alberta, Canada, where an extensive road network is growing, exhibited thresholds in response to road density that would leave otherwise suitable areas unoccupied as a result of conditions in their neighborhood. The approach of Frair et al. (2008), which focused on the environment of individuals and movements and how these scale up to occupancy patterns, is consistent with a hierarchical view of range erosion in the face of threatening processes. While the rich literature on habitat patch occupancy in fragmented landscapes also involves many examples of thresholds (Andren 1994, Fahrig 2001, Radford and Bennett 2004), the key distinction of Frair et al.'s (2008) study is that it defines the home range based on the biology of species as opposed to the pattern of landscape fragments.

Studies seeking to apply source-sink theory to understand distributions of hunted species have tended

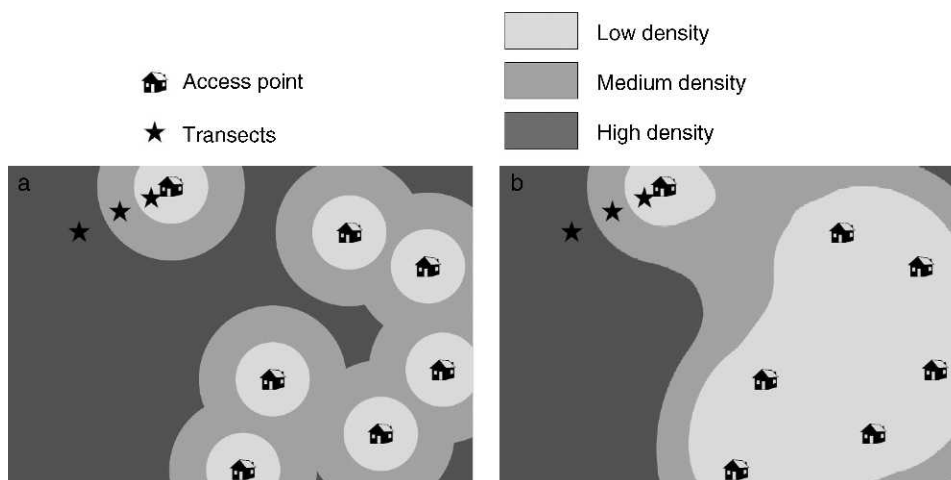


FIG. 2. Densities of the target species (a) based only on distance to access points and (b) based on the percentage of overlap between the threatening process and the scale of the target species in Fig. 1b. Note that neither panel is based on Fig. 1a, and that although panels (a) and (b) differ throughout the landscape, they provide similar results along a hypothetical transect starting from the most remote settlement. As a result, it would be impossible to distinguish the importance of the additive impact of multiple access points based on studies in more remote areas.

to focus on circumstances where the management of different parcels is well differentiated (i.e., hunted vs. non-hunted; Mace and Waller 1988, Novaro et al. 2000, 2005, Naranjo and Bodmer 2007, Robinson et al. 2008) or there are only a few access points (Barnes et al. 1991, Peres and Lake 2003, Blom et al. 2005, Blake et al. 2007). The choice of areas with few access points is important because models based on either the closest access or multiple access points are likely to agree when there are few access points, while disagreeing at higher levels of access. This point is illustrated in Fig. 2 in which the density values at the hypothetical sampling locations in a more remote part of the hypothetical landscape are the same for both models even as the predictions throughout the rest of the landscape vary greatly. This suggests that understanding the effects that the spatial structure of threats will have on wildlife will require that we sample along the spectrum of human influence and consider a variety of hypotheses of the manner in which humans affect the distribution of hunted species.

The African forest elephant (*Loxodonta africana cyclotis*) is an ideal species to test how access affects the distribution of wide-ranging species. Individuals move over large areas on daily, weekly, and seasonal timescales, leaving signs of their presence as they move. Densities of forest elephants are usually based on elephant dung counts because the actual animals are difficult to observe. Understanding how multiple access points influence elephant distributions is becoming increasingly relevant in previously isolated parts of the West and Central Africa forest, where roads and settlements associated with commercial forestry, mining, and petroleum operations are leading to increased access for hunters (Laurance et al. 2006, Blake et al. 2007,

2008). From a conservation point, understanding the relationship between the spatial structure of access points and elephant densities (as estimated from elephant dung counts) is extremely important both in terms of designing and analyzing monitoring programs and in developing management interventions that minimize the impacts of hunting both within and outside of protected areas.

Here we relied on elephant dung count data from within and around five national parks in Central Africa (Blake et al. 2007) to investigate how the spatial structure of access points influences the distribution of *L. a. cyclotis*. More specifically we asked: (1) Are models that consider the cumulative effects of multiple, nearby access points better supported by data than models based on the closest access point only, and are the access-based covariates more important in predicting presence or density conditioned on presence? (2) To what degree and at what scales are threats affecting elephant densities through changes in occupancy (HRSR) or through decreases in local densities conditioned on presence (LPSR)? (3) To what extent do models differ in their predictions of the total quantity of dung and its spatial distribution (i.e., what are the practical implications of different models)?

METHODS AND MATERIALS

Transect data

In order to gain a better understanding of the response of forest elephants to multiple access points we reanalyzed a data set that was previously included in a broader study of the state of forest elephant populations in the Congo Basin (Blake et al. 2007). Three-hundred and eighty-three transects were surveyed for elephant dung in and adjacent to five protected areas

TABLE 1. Distribution of sampling locations among the five countries/protected areas.

Country	Protected area	Number of transects
Cameroon	Boumba Bek	47
Central African Republic	Dzanga (Ndoki and Sangha)	75
Gabon	Minkébé	60
Congo	Nouabalé Ndoki	71
Democratic Republic of the Congo	Salonga	130

Note: Some transects were located outside strictly protected areas.

in five Central African countries (Table 1). While the majority of these transects (339) were 1 km in length, 19 transects in Salonga National Park (NP) were cut short by 12 m to 272 m due to impassable terrain, and 25 of the transects in Dzanga NP were only 300 m in length due to the adoption of a different protocol. Along each transect all signs of elephants and humans were noted, as well as several habitat variables. For our analysis, the response variable was the number of elephant dung piles recorded per transect. Here we report the results of an analysis using dung piles in all freshness categories; however, we found similar qualitative results when we restricted our analysis to different freshness categories. Elephant dung piles are the elephant sign that is predominantly used in estimating forest elephant densities (Barnes 2001). We controlled for differences in the effective area sampled per transect by including its log as an offset in the count portion of the model. Since the predictors in the count portion of the model are linked to the number of dung piles through a log link, including the log of the effective area sampled per transect with the predictors is in effect the same as modeling the density of dung per square kilometer. The effective area sampled per transect was calculated by fitting distance sampling detection functions to the forest elephant dung piles in order to estimate the effective strip width and multiplying this by the transect length. Since each park was surveyed by a different team, we had reason to believe that detection functions might vary between different parks. We tested this assumption by comparing the values of the Akaike Information Criterion (AIC) for a model with separate detection functions to the AIC of a model where the detection function was the same for all parks. Comparison based on AIC strongly favored the model with separate detection functions for each park, and we used the park-specific estimates of effective strip widths associated with these detection functions in further analyses. All detection functions were fit using Distance software (Thomas et al. 2006) with a half normal cosine function. A few dung piles lacked the perpendicular distance required to fit a detection function and were included in the main analysis, but excluded from the estimation of the effective strip width.

GIS data

The locations of roads, populated places, and rivers were obtained from the National Imagery and Mapping Agency's (NIMA) Digital Chart of the World (NIMA

1997). Both river and road data sets were edited to add major roads and rivers that were known to have been omitted or misplaced. Individuals familiar with each of the parks designated which rivers were navigable.

GPS points taken at the beginning and end of each transect were used to define the midpoint of each transect. We then used this location to calculate distances to the nearest river, road, and populated place for each transect. To test whether access points acted additively we first had to define the spatial extent of the effect of each access point. We chose a distance of 20 km based on Blake et al.'s (2007) analyses of the human signs portion of this data set. They found that at this distance from the nearest road the probability of detecting human signs fell below 50% in all areas and the mean probability based on the pooled data was <40%. Although Blake et al. (2007) only considered roads, we also analyzed populated places and observed a similar pattern. Thus, we felt confident in using 20 km for all types of access points. We then created an index of the cumulative effects of multiple access points, $C_{\text{type},r}$, which measured the proportion of a circle with radius, r , which overlapped with the 20-km buffer around the given type (settlement [s], river [ri], or road [ro]) of access point. We calculated this index for rivers, roads, and populated places using a 30 km radius. We chose a 30 km radius as a starting point based on Blake et al. (2008). We also calculated the index for radii of 15 km, 45 km, 60 km, 75 km, and 90 km for roads only in order to determine if the HRSR was operating at larger scales, and if and at what scale the LPSR was operating.

Statistical modeling

Forest elephants travel individually or in small groups of different sizes (usually 2–5 individuals) and make fine-scale habitat selection based on variables such as fruit density and browse quality that are patchily distributed in space and time and unknowable at the scale of this investigation (Walsh et al. 2001, Blake 2002). This behavior would lead to overdispersed dung count data. Avoidance of and/or higher mortality in potential home ranges overlapping with the areas around access points could also lead to a greater proportion of zeroes than expected. To accommodate these two processes, we chose a zero-inflated negative binomial (ZINB) regression model (Welsh et al. 1996). Initial examination of the raw data provided evidence to support our choice as the dung data appeared to be overdispersed and to

contain extra zeros. However, we also tested our initial assumption using a Vuong test (Vuong 1989) by comparing our final models to analogous models using simpler probability distributions that allowed for only overdispersion (negative binomial) or only a separate process producing zeros (zero-inflated Poisson). Vuong tests are a means of comparing non-nested models. Analyses were conducted in R 2.7.2 (R Development Core Team 2008) using the `pscl` package to fit the zero-inflated models (Zeileis et al. 2008) and perform the Vuong test (Jackman 2008) and the MASS (Venables and Ripley 2002) package to fit the standard generalized linear model with a negative binomial distribution. The ZINB regression model allows for separate linear combinations of predictors for the count portion of the model and the zero portion of the model. The separate linear combinations are transformed through $\log(\text{count data})$ and logistic (zero portion) link functions. As mentioned previously, the count data portion of all models included the log of the effective area sampled per transect as an offset.

We had a priori reason to believe that there might be significant differences in abundance between different regions irrespective of our predictors because of differences in environmental conditions and the history of human impacts. For example, human settlements have been present in Salonga for many years, while Minkébé was relatively inaccessible until recently. Following Blake et al. (2007), we considered Nouabalé Ndoki and Dzanga, which are contiguous as a single region and included four region-specific intercepts in the count portion of the regression model for all analyses (i.e., one for Ndoki-Dzanga and one for each of the three other sites).

To assess the effects of the multiple access points on elephant densities relative to the single closest access point (question 1), we tested a set of 21 models that included various combinations of either single or multiple access points as covariates. We also considered a null model that assumed that dung densities were homogeneous across the study areas. The seven covariates included were: (1) the distance to the nearest settlement; (2) distance to the nearest road; (3) distance to nearest river; (4) distance to nearest settlement, river, or road; (5) C_{s30} ; (6) C_{ro30} ; and (7) C_{ri30} . These covariates were first included in the zero portion of the regression model, then in the count portion, and finally in both portions. We used AIC to choose the model that had the strongest support in the data (Johnson and Omland 2004). To assess the distance at which threats affected home ranges or population densities (question 2), we compared 36 models based on all distance combinations (i.e., 15 km, 30 km, 45 km, 60 km, 75 km, and 90 km) of $C_{ro,r}$ in the count and zero portions of the model. We focused on $C_{ro,r}$ since the model that included it had the lowest AIC values in question 1. We used AIC values to calculate Akaike weights for these 36 models. A model's Akaike weight can be

interpreted as the probability that it is the best model given the data and entire model set under consideration (Burnham and Anderson 1998). Akaike weights can also be summed across models containing the same covariate to express the strength of evidence for a particular covariate.

Model predictions: comparison of three models

In order to illustrate the differences in predictions that result from different modeling assumptions we chose three representative models and determined the predicted distribution of dung density and total abundances per region. The three models we chose were the model with the overall lowest AIC, the model with the lowest AIC amongst models based only on nearest access, and a simpler model based only on the negative binomial distribution (as opposed to the ZINB in the first two models) and incorporating the nearest road as a predictor. We chose to include this last model, one which was not in our analysis and which does include zero-inflation, in order to illustrate how the predictions would have differed if we had ignored the excess zeros in our data and assumed that the closest road, instead of the cumulative effects of roads, was the best predictor. To illustrate the density distribution for the four study regions, we broke each region into 1 km²-grid cells and the relevant covariates (distance to closest road, C_{ro45} , and C_{ro60}) were estimated at their centers. We choose this resolution after experimenting with finer and coarser scales and determining that covariates hardly varied between neighboring points at this resolution and that any finer scale made calculations needlessly computationally intensive.

Calculating the expected probabilities of zero, expected count, and expected combined results were relatively straightforward in ArcGIS (ESRI 2008) using the Spatial Analyst tool; however, we also wanted to incorporate prediction uncertainty, particularly for our estimates of abundance. To account for parameter uncertainty in the three separate models we took random draws of parameter values from the multivariate normal distribution described by the variance-covariance matrix and maximum likelihood parameter estimates associated with each model. Since the probability of zero was calculated on the scale of thousands of square meters, we chose to treat each 1-km square as 400 replicates of 2500-m² squares. Therefore, for each draw of parameter values we calculated a prediction for each 1-km² square by first choosing from the binomial distribution given by the predicted probability of occupancy for that 1-km² square and with size equal to 400, and then choosing from the negative binomial distribution predicted for that 1-km² square. These values were then summed to give the prediction for that cell. After this procedure had been repeated for each 1-km² square in the four regions for a given set of parameter values, we determined the predicted abundance for each region and moved on to the next draw of

TABLE 2. Comparison of the ability of 36 models based on our index of the cumulative effects of roads (C_{ro}) to predict both empty transects and the abundances in nonempty transects.

Count portion	Zero portion					
	C_{ro15}	C_{ro30}	C_{ro45}	C_{ro60}	C_{ro75}	C_{ro90}
C_{ro15}	54 (...)	30 (...)	10 (0.004)	7.8 (0.012)	16 (...)	21 (...)
C_{ro30}	48 (...)	27† (...)	8.1 (0.011)	7.3 (0.016)	15 (...)	20 (...)
C_{ro45}	37 (...)	19 (...)	3.0 (<i>0.134</i>)	5.8 (<i>0.033</i>)		
C_{ro60}	30 (...)	13 (<i>0.001</i>)	0.0 (<i>0.615</i>)	8.3 (<i>0.010</i>)		
C_{ro75}	35 (...)	15 (...)	3.0 (0.135)	12.8 (<i>0.001</i>)		
C_{ro90}	40 (...)	19 (...)	6.2 (0.027)	15.1 (...)	30 (...)	38 (...)

Notes: The main entries are the Δ AICs based on this model set, and the values in parentheses are the Akaike weights. The six models in boldface all include C_{ro45} as the predictor of empty transects, and their combined Akaike weights suggest that there is a greater than 90% probability that the best model includes C_{ro45} . There is also >95% probability that the best model includes a predictor of abundance based on C_{ro} measured at the same or greater extent than C_{ro45} (i.e., at 45 km, 60 km, 75 km, or 90 km; models are italicized). Ellipses indicate that the corresponding Akaike weight was <0.001.

† This model is the same as model 22 in the first set (see Appendix), and the high value of Δ AIC (27) illustrates the improvement in the second set of models over the first set.

parameter values. In total, we chose 1000 draws for each of the three models and computed means and standard deviations for each of the four regions based on the 1000 draws. For the best model we also calculated both a mean and standard deviation for each cell. These values were used to check that the means matched with the expected values and to calculate coefficients of variation. The comparison of results from design-based and model-based abundance estimates can lead to greater understanding of the practical significance of model outputs (Hedley and Buckland 2004), so for each region we also compared the average densities predicted by these three models to estimates from a prior design-based analysis of the data (Blake 2005).

RESULTS

1) *Are models that consider the cumulative effects of multiple, nearby access points better supported by data than models based on the closest access point only and are the access-based covariates more important in predicting presence or density conditioned on presence?*—Models based on the cumulative effects of multiple access points were better supported than those based on the nearest points for all three classes of access points (i.e., river, road, and populated place). The best overall model included the index of cumulative effects of roads in the count and zero portions (Model 22 in Appendix); however, the simpler model that included the cumulative effects only in the zero portion differed from model 22 by only 0.9 in its AIC value suggesting that the cumulative effects of roads (as measured at the scale of 30 km) act primarily on patterns of occupancy and not on density. More generally, models based on roads and settlements were better supported than those based on rivers or closest overall access, regardless of whether the cumulative or nearest indices were used. All indices had a larger impact on AIC when they were only included in the zero portion than when they were included only in the count portion.

2) *To what degree and at what scales are threats affecting elephant densities through changes in occupancy*

(*HRSR*) or through decreases in local densities conditioned on presence (*LPSR*)?—The overall best model from this set includes C_{ro45} in the zero portion and C_{ro60} in the count portion, leading to a 27 point decrease in AIC as opposed to the best model considered in the previous set. Vuong tests confirmed that this best model was better than models with the same covariates based on either a negative binomial distribution only or a zero-inflated Poisson distribution only ($P < 0.001$ for both comparisons). Focusing on the support for the covariates in the best model across all models in this set, the data strongly support models incorporating C_{ro45} in the zero portion of the ZINB regression (92.5%) and provide weaker support (62.5%) for C_{ro60} in the count portion; however, while there is only moderate support for C_{ro60} in the count portion, there is over a 95% probability that C_{ro} measured at scales equal to or greater than 45 km (i.e., at 45 km, 60 km, 75 km, or 90 km), should be included as the predictor of the count portion (Table 2).

3) *To what extent do models differ in their predictions of the total quantity of dung and its spatial distribution (i.e., what are the practical implications of different models)?*—Total dung abundance and density estimates by region vary greatly depending on the model used to generate the estimates (Table 3). The predictions of the model based on cumulative effects (the best overall model) are lower than the predictions of the other two spatial models in all four regions, and lower than the design-based estimates in the three regions where estimates are available. Summed over all four regions, the model based on cumulative effects predicts 11.1 million (18%) less dung than the model without a zero portion based on the nearest road and 2.6 million (4.7%) less than the model based on the nearest road in both the zero and count portions. In addition to these differences in the total amount of dung, there are marked differences in the predicted distributions of dung (Fig. 3). In particular, the model based on cumulative effects often predicts sharp gradients in the dung density near edges of the regions. To gain a better understanding of

TABLE 3. Design- and model-based estimates (ZINB, zero-inflated negative binomial regression) of dung density and abundance by region.

Region	Design-based estimate†	ZINB					
		Negative binomial, closest road		Closest road in count and zero		C_{ro60} count; C_{ro45} zero	
		Dung density (piles/km ²)	Abundance (total number of dung piles)	Dung density (piles/km ²)	Abundance (total number of dung piles)	Dung density (piles/km ²)	Abundance (total number of dung piles)
Boumba Bek	NA‡	671 (143)	1 600 000	889 (203)	2 120 000	646 (169)	1 540 000
Dzanga/Nouabalé	724§	755 (95)	6 970 000	745 (75)	6 870 000	625 (60)	5 770 000
Minkébé	5348	5619 (870)	52 300 000	4632 (560)	43 100 000	4613 (555)	42 900 000
Salonga	91.6	102 (18)	2 270 000	112 (21)	2 490 000	81 (18)	1 810 000

Notes: Model-based estimates were obtained by assuming three different models for the distribution of dung. Values in parentheses are standard deviations.

† Standard deviations for design-based estimates are not directly comparable as they include different sources of uncertainty (e.g., uncertainty in effective strip width).

‡ Density estimates were not attempted for Boumba Bek.

§ Dzanga and Nouabalé were originally analyzed separately, and here we report the weighted average based on the respective areas of the two regions.

how the cumulative effects model is arriving at these predictions and what the levels of uncertainty are around the predictions, we decomposed portions of the ZINB predictions and calculated the coefficient of variation (CV) of the aggregate predictions (Fig. 4). These decomposed portions suggest that the zero portion of the model is driving many of the patterns apparent in the overall predictions (Fig. 3), as well as the patterns in the CV.

DISCUSSION

Our results provide support for the hypothesis that wide-ranging mammals respond more strongly to multiple access points for hunters than to the closest single access point. In particular, the probability that any location will be devoid of elephant dung, and thus presumably of elephants, is closely linked to how much of the area within 45 km of that location is within 20 km of roads and/or settlements. The scale of 45 km for this response is strongly supported by the data as opposed to other potential response scales that were considered (15–90 km at 15-km intervals). This scale matches previous estimates of home range dimensions for forest elephants. For example, Blake et al. (2008) found that the average maximum linear displacement, defined as the longest axis of the minimum convex polygon, of 28 forest elephants was 40.3 km.

In addition to the support for HRSR in the zero portion of the ZINB regression, there was good, albeit slightly weaker, support for a response in dung densities to multiple access points at even larger scales (i.e., at the scale of local populations). The overall best model included an index of overlap at the scale of 60 km, and there was a greater than 95% probability that the response was occurring at scales ≥ 45 km. Although this effect was not as pronounced as the HRSR, this may be because declines in local populations occur over longer time intervals than the direct mortality and behavioral response of elephants (avoiding hunted areas and

crowding in other areas) that are associated with the HRSR. Furthermore, because we only have data from one time period and included region-specific intercepts, it is possible that the effects of hunting on densities are included in the regional intercepts (in addition to differences in the natural population ecology of elephants in the different regions). In other words, the LPSR we detected occurred on top of differences in the average densities between different regions that are partially the results of the history of hunting in these regions. For example, Salonga, an area with a long history of high human impact in the immediate landscape, had a much smaller intercept than Minkébé, an area where heavy exploitation of elephants began more recently. Regional intercepts may also reflect variation in dung decay rates. Dung decay rates are known to vary greatly temporally and between different regions. Within each protected area, efforts were made to complete transects over as short a time as possible (typically a few months) to limit the impact of temporal variation. Regional variation in decay rates was harder to control for and we assumed that, while it plays some role in the estimated regional intercepts, it is highly unlikely that it introduced a systematic bias.

As with most models of ecological processes, even the best models considered in this study were still gross approximations (Box 1976, Scott et al. 2002). Our models do not account for regional variation in dung decay rates, the possibility that hunters may be found in areas far from roads (Blake et al. 2007), variation in the degree of protection, local human population density and hunting intensity, or regional differences in the distance elephants and hunters travel (which would lead to differences in how the cumulative effects are calculated). Despite these limitations, models based on the cumulative effect of access points were far better supported by the data than the commonly used alternatives relying only on the nearest road. In addition, the best supported model predicted lower

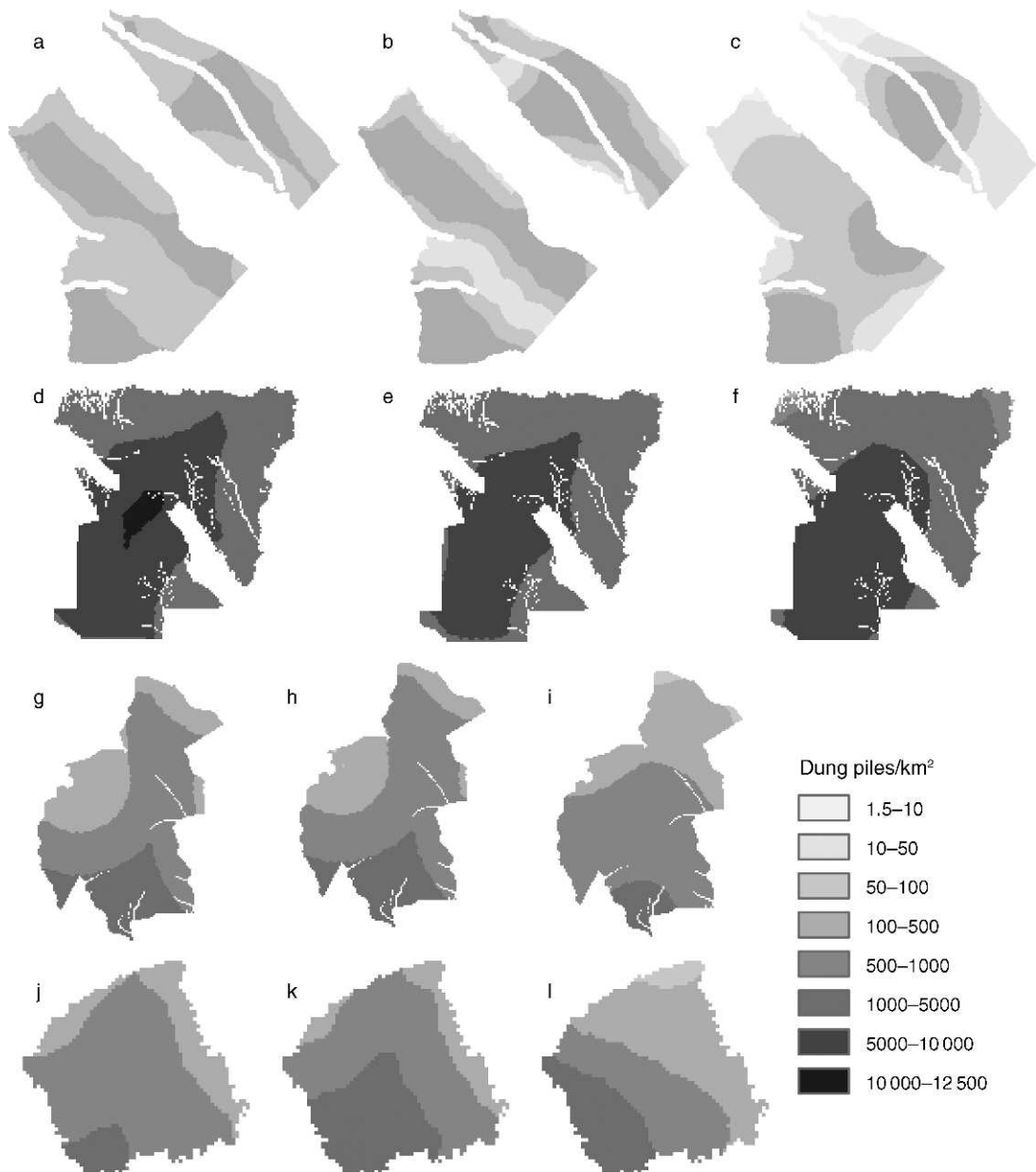


FIG. 3. Density surfaces predicted by three models in the four regions. Within each region (row), left-hand maps (a, d, g, j) show the predictions based on negative binomial only regression with distance to road as the predictor; center maps (b, e, h, k) show the projection based on zero-inflated negative binomial (ZINB) regression with distance to road in both portions; and right-hand maps (c, f, h, l) are based on ZINB regression using the best predictors identified in Table 2 (C_{ro45} in the zero portion and C_{ro60} in the count portion; see *Methods and materials* for a description of index C). The regions from top to bottom are (a–c) Salonga, (d–f) Minkébé, (g–i) Dzanga/Nouabalé, and (j–l) Boumba Bek (see Table 1 for countries). Note that scales used to display the results for the different regions are not the same.

regional abundances than either design-based analyses or model-based analyses based on distance to the closest road (Table 3). Lastly, the best supported model predicted a different distribution of densities within the regions than was predicted by models based on distance to the closest road (Fig. 3).

While the use of an index that includes multiple access points instead of just the nearest access point explains

some of the improvement in our ability to approximate the underlying distribution, another key difference in this study was the use of ZINB regression. This model allowed us to model the separate processes that we believed were responsible for areas that were not occupied and for densities in those areas that are occupied. While a count-based model can account for some zeros, the importance of the zero-inflation portion

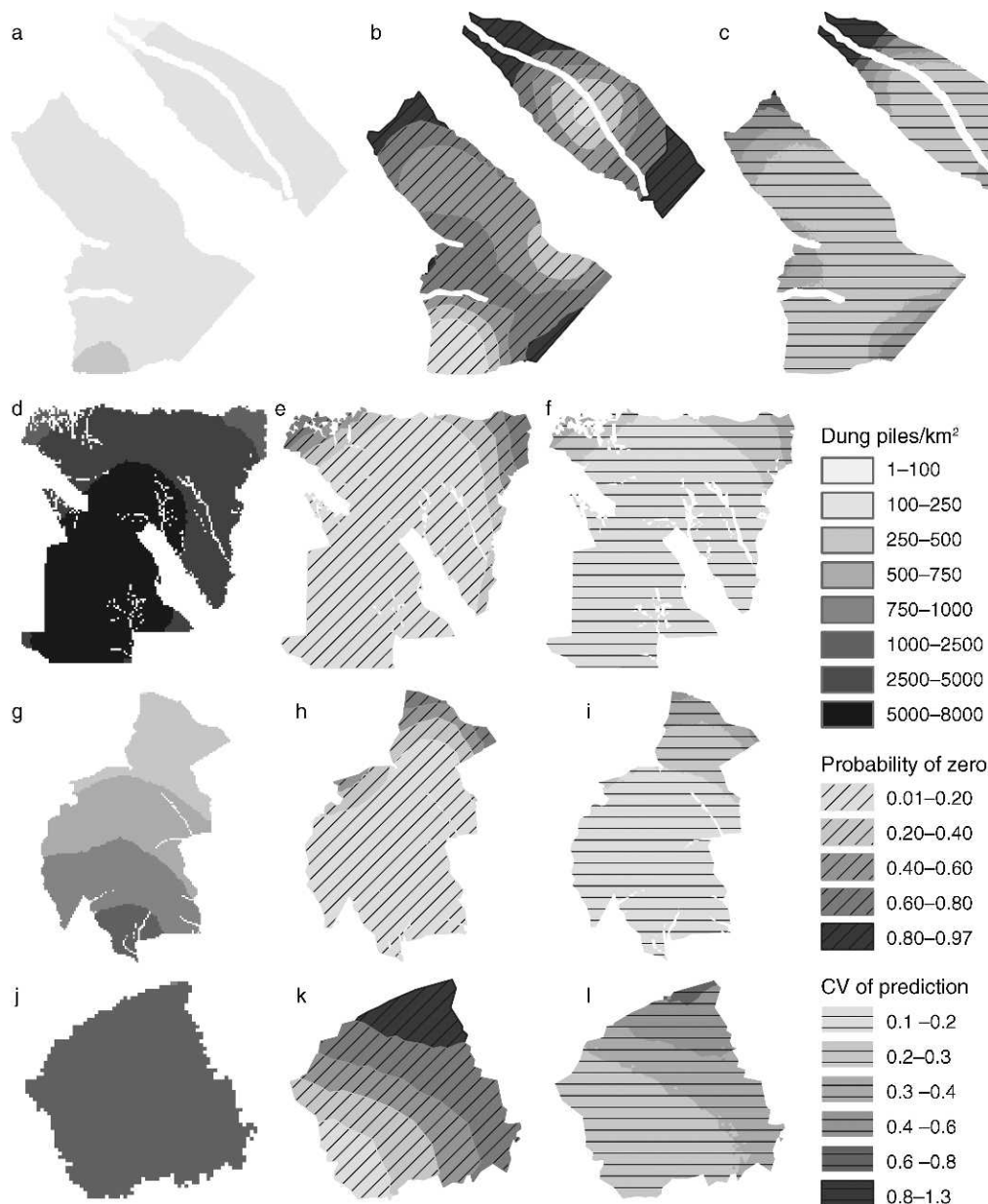


FIG. 4. Decomposition of the best model identified in Table 2. Regions are the same as in Fig. 3. The maps on the left (a, d, g, j) in each region show the prediction from the count portion of the ZINB model, the maps in the center (b, e, h, k) show the prediction from the zero portion of the ZINB model, and the maps on the right (c, f, h, l) use the coefficient of variation (CV) calculated from 1000 simulations of each 1-km square to illustrate the variation resulting from parameter uncertainty. Notice the large roles that zero predictions play in both the overall prediction (maps on the right-hand side of Fig. 3) and in the CV. These estimates of CV do not include uncertainty in the estimates of the effective strip width.

of our best model and the Vuong tests confirm that a two-process model is best supported by the data. In addition to the different predictions offered by a two-process model, this model has interesting implications for how we think of range collapse. In particular, our results are consistent with the belief that range collapse in species with home ranges occurs both through losses at the level of individual home ranges and through declines in the local populations.

Implications for conservation and land use planning

Our study strongly supports previous calls (Laurance et al. 2006, Blake et al. 2007, 2008) to improve road and other infrastructure planning at local and national levels in the Congo Basin. Planning for roads, settlements, and oil and mining infrastructure usually depends on a single criterion: how cost effective is the planned development in the short term. Wilderness areas in the Congo Basin

have shrunk dramatically over the last two decades, and multiple access points are driving ever deeper into formerly inaccessible forests. While any access into wildlife habitat in the absence of effective law enforcement threatens the integrity of wildlife populations, we have shown that proliferation of access points is particularly damaging for wide-ranging species such as forest elephants. As the number of access points increases and the area of available wilderness declines, the costs of adequate policing escalate dramatically. In central Africa today, these costs are almost exclusively borne by grants awarded to conservation nongovernmental organizations (NGOs), and seldom by the private sector and national governments whose development policies and practices create and exacerbate the problem. Until the impact of the geography of access is accepted, understood, and taken into account at the infrastructure planning stage, conservation effectiveness of wide-ranging forest elephants will continue to decline.

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APPENDIX

ΔAIC values for the first set of models and the best model within this set (model 22) (*Ecological Archives* A021-060-A1).