Preliminary survey of forest elephant crossings in Sangha Trinational Park, central Africa

Karen Weinbaum[1]*, Zacharie Nzooh[2], Leonard Usongo[2], Melinda Laituri[1]

[1] Colorado State University, Department of Forestry, Rangeland Watershed Stewardship, Fort Collins, CO 80521, USA
[2] World Wide Fund for Nature, Cameroon Programme Office, PO Box 6776, Yaounde, Cameroon
* address for correspondence: Department of Environmental Science, Policy and Management,
140 Mulford Hall, University of California, Berkeley, 94720-3110, USA; email: kzw@nature.berkeley.edu

Abstract

Wildlife corridors between protected areas play a critical role in maintaining genetic flow between increasingly isolated populations of many species. The importance of wildlife corridors for African savanna elephants (*Loxodonta africana*) has been well investigated. However, African forest elephants (*Loxodonta africana cyclotis*) are difficult to observe in dense tropical vegetation and much less is known about their ecology than about their savanna counterparts. The Sangha River forms an international border between Cameroon, Central African Republic and Republic of Congo and bisects the biologically rich transboundary Sangha River Trinational Conservation Area. The river serves as a primary route for human transportation and trade in the region, and therefore acts as a partial barrier to elephant movement between protected areas. We used a reconnaissance survey technique and dung counts combined with a GIS analysis to survey elephant crossings on the Sangha River. At present, radio-collaring elephants in dense forest is both logistically difficult and expensive, and therefore ground surveys provide a cheaper alternative method for identifying major elephant movement corridors. Results will contribute to a more targeted approach to anti-poaching patrol efforts in the transboundary area.

Additional key words: dung counts, reconnaissance survey, spatial autoregressive model, corridor

Résumé

Les corridors pour la faune sauvage entre les aires protégées jouent un rôle critique dans le maintien d'un brassage génétique entre les populations de plus en plus isolées de nombreuses espèces. L'importance des corridors pour les éléphants de savane africains (*Loxodonta africana*) a déjà été bien étudiée. Cependant, les éléphants africains de forêt (*Loxodonta africana cyclotis*) sont difficiles à observer dans la végétation tropicale dense, et l'on en sait beaucoup moins sur leur écologie que sur celle de leurs homologues de savane. La rivière Sangha constitue la frontière internationale entre le Cameroun, la République centrafricaine et la République du Congo et donc coupe l'aire de conservation du Trinational de la Sangha qui est biologiquement très riche. La rivière est la principale voie de transport et de commerce dans la région et elle agit partiellement comme une barrière qui freine les déplacements des éléphants entre les aires protégées. Nous avons utilisé une technique d'étude par reconnaissance et le comptage des crottes combinés avec une analyse SIG pour étudier les traversées de la Sangha par les éléphants. Pour le moment, la pose de colliers radio à des éléphants dans la forêt dense est à la fois logistiquement difficile et coûteuse, et les investigations au sol sont une méthode alternative moins chère pour identifier les principaux corridors par où passent les éléphants. Les résultats vont contribuer à une approche plus ciblée des efforts de patrouilles anti-braconnage dans la zone transfrontalière.

Mots clés supplémentaires : Comptages de crottes, reconnaissance, modèle autorégressif spatial, corridor

Introduction

Wildlife ranges of many species are becoming increasingly fragmented and constricted into isolated protected areas as anthropogenic land use expands. This is particularly problematic for species that range widely outside protected area boundaries or are migratory. Corridors between viable populations are regarded as one of the best solutions to mitigating problems posed by fragmentation (Beier and Noss 1998; Tewksbury et al. 2002). Corridors are believed to facilitate wildlife dispersal and migration between safe population havens, thereby enhancing genetic flow and thus the potential for species persistence (Taylor et al. 1993; Beier and Noss 1998; Chetkiewicz et al. 2006). In regions where wildlife habitat is fragmented by roads and railway lines, wildlife corridors are increasingly being used to reconnect otherwise blocked passages (Trombulak and Frissell 2000; Clevenger 2005).

The African savanna elephant (*Loxodonta africana* [Blum., 1797]) is a long-distance and seasonal migrant. Savanna elephant population movements have been well studied, either through aerial surveying, radio- and satellite-collar monitoring (Thouless 1995; Osborn and Parker 2003), indirect indices (de Boer et al. 2000), or a combination of interviews with local people and field observation (Mpanduji et al. 2002). Savanna elephants are known to travel up to 450 km (Douglas-Hamilton et al. 2005) and their home ranges vary from 200 to 10,700 km² (Blake et al. 2001). Range corresponds with size of protected area and therefore it is not surprising that whole populations of elephants will travel beyond park borders to sustain themselves. Habitat corridors allow elephants to move between protected areas (Johnsingh and Williams 1999; Osborn and Parker 2003; Douglas-Hamilton et al. 2005).

Much less is known about forest elephant *(L. africana cycloti*s [Matschie, 1900]) movements, however. Genetic evidence has recently confirmed the separation of the African elephant (formerly recognized as *L. africana* with two subspecies) into at least two distinct species: savanna elephants *(L. africana)* and forest elephants *(L. cycloti*s) (Roca et al. 2001), and even a third, West African species, has been proposed (Eggert et al. 2002). Forest elephants play a keystone role in equatorial Africa's tropical forests, structuring tree species composition and physiognomy through seed dispersal (Western 1989), opening up clearings around salt licks and forest gaps, and engineering major paths within the forests subsequently used by other animals and humans (Blake and Inkamba-Nkulu 2004). Forest elephants make up most of mammalian biomass (52–89%) in the African tropical forest ecosystem, underscoring their importance in ecosystem function (White 1994a). They are often one of the first mammalian species to be hunted to local extinction, making them an important indicator species of hunting pressure (White and Edwards 2000).

Unlike savanna elephant populations that can be censused and monitored by aerial surveying, forest elephant ecology is often extrapolated from indirect methods, most commonly using dung counts as a proxy for elephant abundance (White 1994b; White and Edwards 2000), but also through identification of individual elephants at a small number of forest clearings (Turkalo 1996). That the understanding of forest elephant ecology remains low relative to that of the savanna elephant is largely due to logistical dificulty in sampling large, remote swaths of rainforest, the dense canopy cover that precludes aerial surveillance, and habitat that is located in countries often beleaguered by corruption and political strife (Blanc et al. 2003). Seasonal and cross-border movements are additional confounding factors when trying to understand the ecology of a species from static dung counts. VHF and GPS collaring of forest elephants has begun to shed light on home range size, seasonal migration and ranging behaviour. However, collaring in tropical humid forest conditions is still logistically difficult, expensive and subject to relatively high rates of equipment failure (Blake et al. 2001).

Past forest elephant survey efforts have focused on estimating elephant population numbers (Fay 1991; Fay and Agnagna 1991; Barnes et al. 1995b; Hall et al. 1997), and how elephant distribution correlates with human abundance (Barnes et al. 1991; Fay and Agnagna 1991; Hall et al. 1997). White (1994b) noted that elephant movements and densities were strongly correlated with the seasonal fruiting phenology of *Sacoglottis gabonensis*, a fruit elephants greatly favour. Preliminary data from radio-collaring is showing that elephants spend significant time outside protected areas (Usongo 2003; Douglas-Hamilton et al. 2005), traverse national park territories and may have minimum home ranges of 800–1000 km² (Blake et al. 2001). Despite emerging reports of elephants crossing country borders and major rivers (Ekobo 1995; Usongo 2003), little is still known about sea-

sonal migratory behaviour or major corridors (Barnes 1999).

The objectives of this study are to identify major forest elephant crossings on the Sangha River between Cameroon, Republic of Congo (Brazzaville), and Central African Republic using dung count methodology and to predict environmental and anthropogenic determinants of elephant corridors in the study region. This study complements existing research work on trans-boundary monitoring of radio-collared forest elephants and will contribute to more targeted anti-poaching patrols in the study area.

Materials and methods

To identify major elephant crossing points and model ecological and anthropogenic determinants of elephant distribution in the study region, we used the directed reconnaissance survey method to collect dung encounter rates as an index of relative elephant abundance. This method was developed to survey elusive mammals in dense humid African rainforests (White and Edwards 2000), and dung encounter rates were quantified as the number of dung piles per kilometer surveyed. We also collected georeferenced

data on active and abandoned human settlements and obtained vegetation class data from Landsat Thematic Mapper (TM) satellite imagery. Our models used dung encounter rates as the dependent variable, and both active and abandoned human settlements and percentage of vegetation classes as independent variables. Because of possible autocorrelation in the data, we compared ordinary least squares and a spatial autoregressive model to examine significant predictors of elephant abundance indices.

Study area

The Sangha Trinational Park Conservation Area is formed where the borders of three protected areas in three central African countries meet—the Dzanga-Sangha Dense Forest Special Reserve and Dzanga-Ndoki National Park in south-western Central African Republic, Nouabalé-Ndoki National Park in northern Republic of Congo (Brazzaville), and Lobeke National Park in south-eastern Cameroon, contributing to a contiguous protected forest of over 10,000 km^2 (fig. 1).

The vegetation is representative of the northern fringes of the Guinea–Congolean forest block with
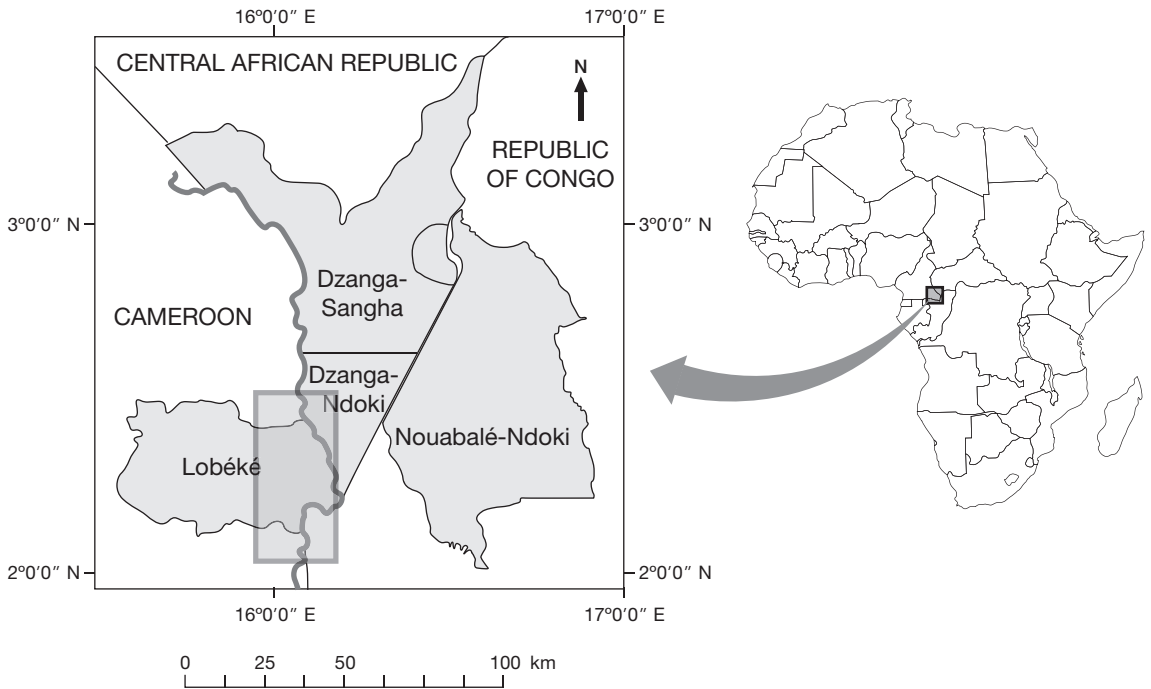

Figure 1. Sangha Trinational Park region, Central Africa. Box indicates study area.

semi-deciduous forest on sandy clay soils, evergreen forest on red clay soils, and transitional evergreen and semideciduous forest (Letouzey 1985; Ekobo 1995). The climate is transitional between the Congo-equatorial and subequatorial zones with a mean annual rainfall of 1400–1500 mm (Ekobo 1995; Blake 2002a). Rainfall is bimodal with peaks in June and October and a main dry season from December to March, with 100–120 rainy days per year. The average daily temperature is 24 ºC with little seasonal variation (Blake 2002a).

Field methods

Mammal surveys in the African rainforest are traditionally carried out using the line transect method, considered the most efficient way of sampling large areas (White and Edwards 2000; Buckland et al. 2001). Line transects in rain forest are cut through vegetation following a compass bearing, and either live sightings or indirect indices (e.g. nest or dung counts) are recorded. There are several drawbacks to this method; it is time-consuming, expensive (considering logistics of labour and transportation), and detrimental to the forest by directly damaging the vegetation and by facilitating hunter access into formerly unpenetrated forest (White and Edwards 2000).

The reconnaissance modification of line transect sampling (hereafter 'recce') for humid tropical forest surveying has recently been developed (Walsh and White 1999; White and Edwards 2000; Walsh et al. 2001). In a recce survey, the observer follows pre-existing paths or the path of least resistance through the brush whenever possible, with less than 45º deviance in either direction from a compass bearing. Advantages of this method are faster travel (allowing more distance to be covered) and less physical damage to vegetation. The main disadvantage is that this method may produce biased results because the survey technique is not random and may not be representative of all vegetation or habitat types. However, Walsh and White (1999) compared paired 1-km recce and line transects of elephant dung in several central African forest sites and found the slope of the relationship between pairs to be 0.98, indicating a nearly one-to-one relationship, for a much higher sampling efficiency. In this study we use mean dung encounters per kilometre of recce survey as an index of relative abundance. However, if true animal density estimates are desired, the directed reconnaissance survey can be combined with traditional transects

(using a correction factor for inherent site-dependent bias) and distance methods used to calculate density estimates (Walsh and White 1999; Buckland et al. 2001; Walsh et al. 2001). Dung counts are the standard proxy for estimating relative elephant abundances, density estimates, and distribution in forests (Barnes et al. 1991; White and Edwards 2000). They are undertaken along line and/or recce transects. For each dung pile, the age of dung, vegetation type and other animal and human signs are recorded.

In this study we used two 60-km long parallel recce surveys (hereafter 'transects') along both banks of the Sangha River (fig. 2a): on the Cameroonian border (western bank of the Sangha River, hereafter 'west bank'), and the Central African Republic and Congolese border (eastern bank of the Sangha River, hereafter 'east bank'). Surveys were conducted at a distance of 50–100 m from the Sangha River on both its east and west banks, within and adjacent to Lobeke National Park (south-east Cameroon), Nouabalé-Ndoki National Park (northern Congo) and Dzanga-Ndoki National Park (southern Central African Republic), between March and May 2003. Surveying forays were 3–10 days in the forest, with three local assistants, covering a total of 120 km. Each datum was georeferenced and entered directly into a Palm Pilot with CyberTracker Software 2.72 and a GPS Navigator attachment, which allowed continuous GPS coverage and data storage.

Data analysis

We buffered each transect line at 200 m in ArcGIS v9.1, and divided these into kilometre-long segments. The unit of analysis was the number of dung counts per kilometre (log transformed). These were used to calculate the correlation between mean dung encounter rates on each side of the river, as the dependent variable in modelling determinants of elephant abundance (by indirect dung encounter rates).

We also used ArcGIS to count the number of abandoned and active villages in each segment, and tabulate percentage of types of vegetation for each kilometre segment, based on 15 classes of a supervised 30 x 30-m resolution Landsat TM image. These types were consolidated into nine vegetation classes based on ecological similarity, to integrate land classes with low representation. The final class types were monodominant evergreen *Gilbertiodendron dewevrei* forest (> 90% canopy cover), mixed

semi-evergreen closed forest (> 90% canopy cover), mixed semi-evergreen semi-open forest (60–90% canopy cover), mixed semi-evergreen forest with understorey dominated by *Megaphrynium* spp. (very open), semi-evergreen mixed species tall swamp, monodominant *Raphia* swamp, savanna, agriculture, and bare soil and roads.

We evaluated the relative influence of ecological and anthropogenic determinants on the spatial distribution of elephants (according to dung distribution) in the study area using multiple regression. Most natural ecological phenomena display spatial structuring and typically ecological phenomena are positively autocorrelated in space, so that nearby points have more similar values than would be expected at random (Legendre 1993; Carroll and Pearson 2000; Lichstein et al. 2002). If autocorrelation is present, the value at one location can be partly predicted by values at nearby locations, violating the basic assumption of independence in most common statistical tests and predictive models used in ecology (Carroll and Pearson 2000). Violation in the assumption of independence can lead to false conclusions in interpreting statistical results, including failure to discover existing relationships, false identification of non-existing relationships and inaccurate predictions (Carroll and Pearson 2000). The continuous nature of line-transect sampling and recce surveys, designed to maximize data collection with logistical efficiency, also increases the chances of sampling autocorrelated data. Therefore, we tested for the presence of spatial autocorrelation in the data using Moran's I and Geary's C statistics. Once detected, spatial autocorrelation can best be dealt with using spatial autoregressive models (Legendre 1993; Carroll and Pearson 2000; Lichstein et al. 2002).

We used the log transformed number of dung counts per kilometre segment as the response variable, and a dummy variable for the east–west transect, latitudinal and longitudinal

coordinates, presence of abandoned and active villages, and nine vegetation types. We compared the ordinary least squares (OLS) method with three spatially autoregressive models—spatial lag, spatial error, and exponential autoregressive (Carroll and Pearson 2000; Lichstein et al. 2002)—which make slightly different assumptions about how to model spatial effects.

An exponential covariance structure was chosen from available PROC MIXED spatial correlation models based on lowest Akaike's Information Criterion. For all models, non-significant vegetation variables were removed with stepwise selection and we
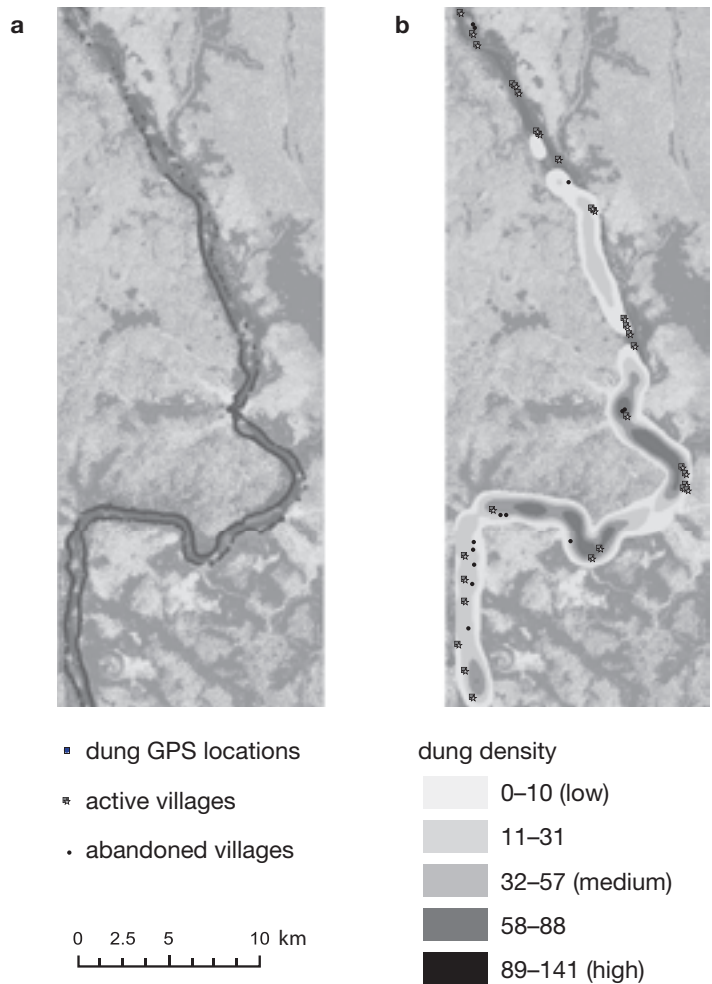

Figure 2. a) GPS locations of dung counts recorded on east and west transects of Sangha River; b) final density map of elephant crossing locations (dung counts per km²).

checked for and removed collinear variables based on a multicollinearity index and cross-correlation between independent variables (SAS v9.1, Geoda 0.95i). We used minimum AIC's to select the most parsimonious model.

Results

A total of 120 km of transect segments were conducted, 60 km on the west bank of the Sangha River (Cameroon), and 60 km on its east bank (Central African Republic and Congo). In all, 3545 dung piles were encountered (2572 on the west bank and 973 on the east bank). After harmonizing start and finish points on both transects, 59 adjacent transect segments on each side of the river were used for this analysis, with 2570 dung piles on the western transect and 960 on the eastern transect. Figure 2b shows the final map of elephant corridors based on dung counts.

Although separated by no more than 0.5 km in most places, the mean dung count was significantly higher on the west bank (43.56 ± 4.25 SE per km) than on the east bank (16.27 ± 2.12 SE per km, $t = 5.75$, $P < 0.0001$, fig. 3). The correlation coefficient (Pearson product moment) of the relationship between dung counts on the east and west bank before adjustments for spatial autocorrelation in the residuals was positive and significant ($r = 0.6385$, $F = 39.23$, $P < 0.0001$) (fig. 4).

Dung counts per kilometre between each transect were significantly correlated with one another, and each transect alone also exhibited internal trends. The west bank was described by a negative second-order polynomial equation ($R^2 = 0.8374$). This showed first an increasing and then a decreasing trend in dung density along the transect in a north-to-south direction. The east bank was also described by a negative second-order polynomial equation ($R^2 = 0.6395$), with a general increasing trend from north to south along the transect (fig. 5).

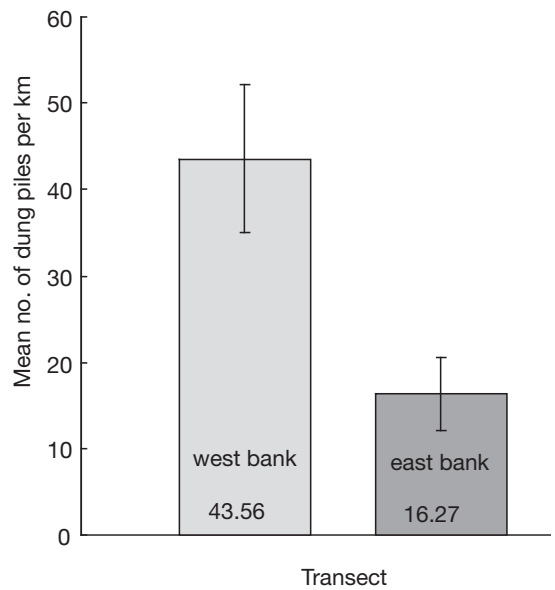The Moran's I and Geary's C tests for autocorrelation in continuous data revealed the

Figure 3. Mean dung pile density per kilometre of transect, west and east banks (error bars indicate 95% confidence).

presence of significant autocorrelation in the residuals of the data: Moran's $I = 0.8632$, $P < 0.0001$, Geary's $C = 0.2056$, $P < 0.0001$, for the west bank; and Moran's $I = 0.7932$, $P < 0.0001$, Geary's $C =$
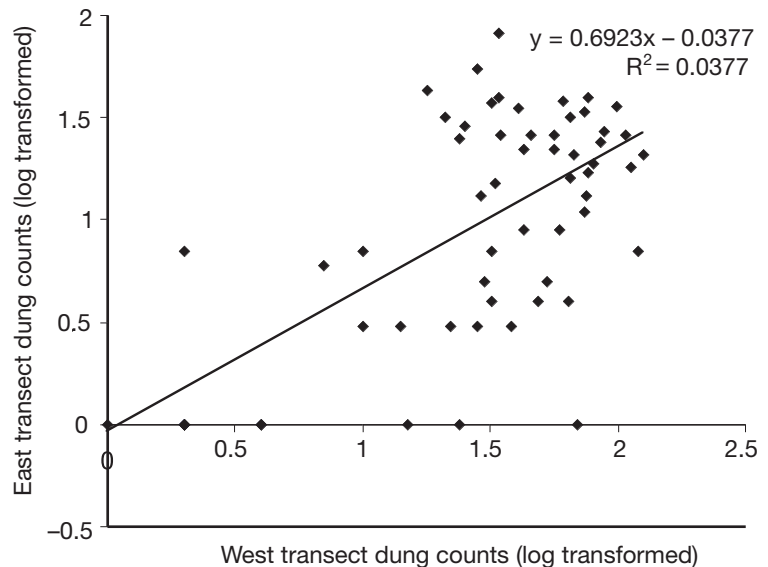
Figure 4. Correlation between east bank and west bank, $r = 0.6385$.

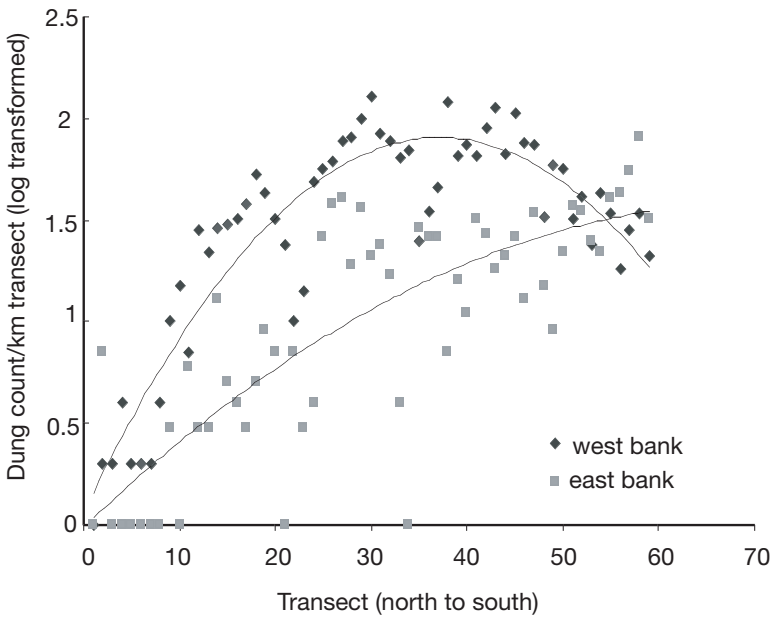On the figure: $y = 0.6923x - 0.0377$, $R^2 = 0.0377$

Figure 5. Dung pile counts per kilometre transect from northern to south-
ern end of each transect. Fit trend lines for the west bank are described
by the equation $y = -0.0013 \times 2 + 0.0995x + 0.0588$ ($R^2 = 0.8374$), and
for the east bank $y = -0.0003 \times 2 + 0.0455 - 0.0123$ ($R^2 = 0.6395$).

0.3246, $P < 0.0001$, for the east bank; thus violating
the assumption of most common statistical methods
of independent errors (Legendre 1993; Lichstein et
al. 2002). Therefore, a spatial *t*-test (Reich and Davis
2003) was used to compare means, which also showed
significant differences in mean counts ($t = 14.31$, $P <
0.0001$). Autocorrelation function plots, which reflect
how much correlation is present between lagged
observations for each transect, also demonstrate sig-
nificant positive correlation in successive counts, up
to a distance (lag) of about 8 km in both cases.

Comparison among models

Parameter estimates among the OLS model and three
autoregressive models were similar, so we discuss here
only the OLS and best fit (lowest AIC) auto-regressive
model. According to the overall lowest AIC ranking,
the spatial error autoregressive model provided the
best fit to the data and accounted for 85.6% of the
observed variability (AIC = 28.42, $R^2 = 0.8561$, table
1). All models showed highly significant 1) difference
in mean dung density between transects, 2) increase
in dung density when moving southward along the
transects, and 3) positive correlation with mixed

species tall swamp and mono-
dominant evergreen *Gilbertio-
dendron dewevrei*. Most models
predicted a significant positive
correlation with abandoned vil-
lages, negative correlation with
active (currently inhabited) vil-
lages, and positive correlations
with monodominant *Raphia*
swamp, mixed semi-evergreen
closed forest and mixed semi-
evergreen, semi-open forest.

Discussion

Though separated by not more
than 500 m in most places,
there was a significantly higher
number of dung piles per kilo-
metre on the west bank than on
the east bank, indicating signifi-
cantly higher elephant densities.
These results may be partly
explained by previous logging
regimes in the area, or different current park manage-
ment strategies. Large areas of the Cameroonian side
have previously been logged, including up to 60% of
the national park's territory (L. Usongo, unpublished
data). Elephant preference for secondary vegetation has
been well documented (Barnes et al. 1991, 1995a) and
is seen in other species as well such as forest buffalo
(Blake 2002b) and gorillas (Matthews and Matthews
2004). Additionally, each park is managed by different
government wildlife institutions and supported by a
different non-governmental organization (NGO). This
may have more direct impact locally if management
styles and strictness of anti-poaching efforts vary.

In addition to the generally higher dung-encoun-
ter rates on the west bank, it was interesting to note
another difference between trends in each transect:
the significant negative polynomial trend on the west
bank (first increasing and then decreasing at the south-
ernmost end of the transect), and the increasing trend
on the east bank (fig. 5). We suspect two reasons for
these trends: first, the presence of a relatively large
logging town (pop. ~8000) about 15 km north of the
transect lines may negatively affect the distribution
of forest elephants in the northern portion of both
transects (and as noted by Barnes et al. (1995), 'man

Table 1. Parameter estimates and significant level of OLS and spatial autoregressive models with inverse-distance weight matrix (spatial lag and spatial error), and exponential covariance structure (exponential autocorrelation model)

Variable	OLS model	Simultaneous autoregressive (spatial lag model)	Simultaneous autoregressive (spatial error model)	Exponential autocorrelation model
Constant	−0.0400 ± 0.4648	−0.4709 ± 0.4201	−0.1394 ± 0.3773	0.0958 ± 0.3983
East–west	−0.4110 ± 0.0796***	−0.4451 ± 0.0702***	−0.5087 ± 0.0660***	−0.5320 ± 0.0676***
UTM northing	−1.2482 ± 0.1981***	−1.0068 ± 0.1884***	−1.2351 ± 0.2159***	−1.2346 ± 0.2642***
UTM easting	0.4553 ± 0.0927***	0.3754 ± 0.0852***	0.4904 ± 0.1248**	0.4799 ± 0.1842*
Abandoned villages	0.0681 ± 0.0269*	0.0640 ± 0.0238**	0.0640 ± 0.0199**	0.0589 ± 0.0212**
Active villages	−0.0626 ± 0.0249*	−0.0546 ± 0.0220*	−0.0309 ± 0.0183	−0.0251 ± 0.0192
Mixed species tall swamp with closed canopy	1.9743 ± 0.4515***	2.0183 ± 0.3985***	2.0866 ± 0.3641***	1.8636 ± 0.3726***
Raphia swamp	1.4938 ± 0.4702**	1.6068 ± 0.4147***	1.6306 ± 0.3800***	1.4442 ± 0.3930**
Gilbertiodendron dewevrei forest	2.3856 ± 0.5240***	2.4460 ± 0.4627***	2.5646 ± 0.4274***	2.2504 ± 0.4422***
Savanna	1.4894 ± 2.3030	2.3084 ± 2.0344	1.9537 ± 1.8609	1.4136 ± 1.8901
Agriculture	0.3948 ± 1.4973	1.1194 ± 1.3213	2.3708 ± 1.1771*	1.8977 ± 1.2129
Bare soil; roads	1.1723 ± 0.7701	1.1414 ± 0.6799	1.2476 ± 0.5944*	1.0414 ± 0.6116
Mixed species semi-evergreen, understorey *Megaphrynium* spp.	4.1669 ± 1.5112**	3.8130 ± 1.3330**	2.1455 ± 1.2133	1.9405 ± 1.2257
Mixed species semi-evergreen forest (closed)	2.4440 ± 0.8184**	2.5254 ± 0.7229***	1.7143 ± 0.7242*	0.6391 ± 0.7484
Mixed species semi-evergreen forest (semi-open)	2.4528 ± 0.7775**	2.6237 ± 0.6857***	2.9603 ± 0.6374***	2.8951 ± 0.6304***
Lambda			0.4575 ± 0.0667***	
*R*²	0.7999	0.8217	0.8561	
AIC	52.2414	44.1345	28.4241	29.80

Geoda 0.9.5-i5, SAS v9.1, S-PLUS 2000, Reich and Davis 2003
*$P \leq 0.05$, **$P \leq 0.01$, *** $P \leq 0.001$, AIC based on maximum likelihood

determines the distribution of elephants'). These trends may also be partly explained by NGO presence (Wildlife Conservation Society) on the southern end of the east bank transect (Congo) near the logging town of Kabo. Locals claim that anti-poaching laws there have been strictly enforced on the Congo side of the river. The act of strictly enforcing anti-poaching laws on one side of an international border may chase a number of poachers to the other side of the border where there is less on-the-ground enforcement.

The regression models in this study linked observed dung counts per kilometre to explanatory human and environmental variables, to identify potential determinants of elephant crossings. All models showed highly significant 1) difference in mean dung density between transects, 2) increase in dung density when moving southward along transects, and 3) positive correlation with mixed species tall swamp and monodominant evergreen *G. dewevrei*. Most models predicted a significant positive correlation

with abandoned villages, negative correlation with active (currently inhabited) villages, and positive correlations with monodominant *Raphia* swamp, mixed semi-evergreen closed forest and mixed semi-evergreen, semi-open forest (table 1).

The regression models revealed patterns similar to those in other published accounts. All the models predicted significant positive trends of elephant dung with abandoned camp sites (secondary vegetation), and two of the models predicted significant negative trends with sites presently occupied by humans (generally small clusters of housing). Previous research has also found preference of forest elephants for secondary or disturbed vegetation (Barnes et al. 1991; Barnes et al. 1995a), and elephant avoidance of active human settlement (Barnes et al. 1991; Fay and Agnagna 1991; Hall et al. 1997). All models showed strong positive correlation with monodominant evergreen *G. dewevrei*. Of the Caesalpiniaceae family, *G. dewevrei* forms extensive single-species stands in the Congo Basin, commonly in riparian areas (Blake and Fay 1997). It is a supra-annually mast-fruiting tree and elephants likely receive high payback from foraging on seeds of *G. dewevrei* in mast-fruiting years. Mast-fruiting refers to the intermittent and synchronous production of large quantities of fruits by a community of plants over long intervals (Numata et al. 1999). Both swamp vegetation types (mixed species tall swamp and monodominant *Raphia* swamp) were also consistently significant predictors across models. Swampy vegetation types may offer large quantities of herbaceous browse that are unavailable in more closed forest habitat types (Barnes et al. 1991). Finally, mixed semi-evergreen closed forest and mixed semi-evergreen forest with understorey dominated by *Megaphrynium* spp. were significantly correlated with elephant dung counts in half of the models. These semi-evergreen forests ranked highest in a list of 23 evaluated for fruit trees favoured by elephants and exhibiting high elephant densities. Additionally, at least one author describes that the highest consistent density of forest elephants yet recorded (ca. three individuals ha^{-1}) was in the Marantaceae (*Megaphrynium* spp.*)* forest of Lopé Reserve, Gabon (White 1994a), a vegetation type for which half the models predicted positive correlation.

As suspected, the transect data exhibited strong autocorrelation. The recognition that most natural ecological phenomena have spatial structure (e.g., patchiness and gradients) (Legendre 1993; Lichstein et al. 2002) continues to be relatively ignored in ecological research in general and in transect studies in particular, and can potentially have serious ramifications in parameter and trend estimations. The OLS model was compared with various spatial models that in addition to modelling independent variables model the correlated residuals. Differences between models proved to be relatively minor in our study, with strong overlap in parameter estimates and significance levels. While parameter estimates were similar among the models, AIC model selection favoured a spatial model, which accounted for over 85% of the variability observed in dung density effects. The autocorrelation function plot revealed that the transect data are autocorrelated up to a distance of 8 km. This suggests that future transect work in this region for forest elephants should either be spaced out at distances larger than 8 km apart for independent sampling units or analysed using autoregressive models. Any data from similar survey work should be examined for autocorrelation.

The Sangha Trinational Park conservation area provides habitat for some of the largest intact populations of large mammals, notably forest elephants and western lowland gorillas (*Gorilla gorilla gorilla*). Initial results from radio-collared forest elephants show that home ranges of elephants in Sangha Trinational Park go far beyond protected area boundaries, with some individuals travelling more than 150 km outside the national park boundary and spending at least 40–60% of their time in surrounding land-use zones, primarily logging concessions (Blake et al. 2001; Blake 2002a; Usongo 2003). Any protection effort by park authorities to save elephant populations must include participation of all stakeholders in the surrounding use zones including logging companies. Effective transboundary protected areas will also require full coordination between participating country national park staff and conservation NGOs in monitoring and surveillance of wide-ranging species to adequately ensure their survival.

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