



Effects of Landscape Features on the Distribution and Sustainability of Ungulate Hunting in Northern Congo

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Abstract: *Understanding the spatial dimensions of hunting and prey population dynamics is important in order to estimate the sustainability of hunting in tropical forests. We investigated how hunting offtake of vertebrates differed in mixed forest and monodominant forest (composed of *Gilbertiodendron dewevrei*) and over different spatial extents within the hunting catchment around the logging town of Kobo, Congo. In 9 months of recall surveys with hunters, we gathered information on over 1500 hunting trips in which ungulates were 65% of the species killed and 82% of harvested biomass. Hunters supplied information on animals killed and the hunting trip, including the area visited (i.e., hunting zone; 11 separate zones within a 506 km² catchment or commonly hunted area). Over 65% of all animals were killed in monodominant forest, which made up 28% of the hunting catchment, and zones with small amounts of monodominant forest were used most frequently by hunters. Given the large offtakes from monodominant forests, we suggest that animal dispersal may be maintaining high, localized harvests in these areas. We believe hunters preferred to hunt in monodominant forest because the understory was accessible and that areas with small amounts of monodominant forest and large amounts of mixed forest were more productive. The variation in hunting pressure we found between and within hunting zones differs from past examinations of spatial variation in hunting offtake, where entire hunting catchments were considered population sinks and areas with low to no hunting (no-take zones) were outside hunting catchments. Future use of no-take zones to manage hunting should incorporate variability in offtake within hunting catchments.*

Keywords: central Africa, Congo, duiker, hunting, source-sink, ungulate

Efectos de las Características del Paisaje sobre la Distribución y Sustentabilidad de la Cacería de Ungulados en el Norte de Congo

Resumen: *El entendimiento de las dimensiones espaciales de la cacería y la dinámica de la población presa es importante para estimar la sustentabilidad de la cacería en bosques tropicales. Investigamos como difirió la cacería de vertebrados en bosque mixto y en bosque monodominante (compuesto de *Gilbertiodendron dewevrei*) y en extensiones espaciales diferentes en la zona de cacería alrededor del pueblo maderero de Kobo, Congo. En 9 meses de entrevistas con cazadores, recolectamos información de más de 1500 viajes de cacería en los que 82% de la biomasa y 65% de las especies cazadas fueron ungulados. Los cazadores proporcionaron información sobre los animales cazados y el viaje de cacería, incluyendo el área visitada (i.e., zona de caza; 11 zonas separadas en el área común de cacería de 506 km²). Más de 65% de los animales*

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fueron cazados en el bosque monodominante, lo que correspondió a 28% de la zona de cacería, y las zonas con superficie pequeña de bosque monodominante fueron utilizadas más frecuentemente por los cazadores. Debido a las capturas en los bosques monodominantes, sugerimos que la dispersión de animales puede estar manteniendo la captura elevada y localizada en estas áreas. Creemos que los cazadores prefirieron cazar en bosque monodominante porque el sotobosque era accesible y que las áreas con superficies pequeñas de bosque monodominante y grandes extensiones de bosque mixto fueron más productivas. La variación en la presión de cacería que encontramos entre y dentro de las zonas de cacería difiere de estudios anteriores de la variación espacial de la captura por cacería, en los que zonas de cacería completas fueron consideradas como vertederos y las áreas donde no se permitía la cacería estaban fuera de las zonas de caza. El uso futuro de zonas sin autorización para la cacería para el manejo de la caza debería incorporar la variabilidad de captura dentro de las zonas de caza.

Palabras Clave: África Central, cacería, Congo, duiker, fuente-vertedero, unglado

Introduction

Worldwide, one of the greatest threats to persistence of vertebrates in tropical forests is unsustainable hunting (Milner-Gulland et al. 2003). Unsustainable hunting is of special concern in the forests of the Congo Basin, where most of the 30 million inhabitants rely on wild animals for protein (Wilkie & Carpenter 1999). The number of animals harvested has risen throughout central Africa as growing and increasingly sedentary human populations have adopted more efficient hunting techniques, such as wire snares and shotguns, and increased their participation in market economies (Fa & Brown 2009). Increased hunting offtakes, as measured by number of animals killed, are more likely where extractive industries such as logging and oil exploitation attract immigrants and lead to expanded road networks, which increases consumption and trade of wild animals (Wilkie et al. 1992; Thibault & Blaney 2003).

Although the effects of hunting on population viability are well documented, understanding how heterogeneity in hunting pressure combines with variation in ecological communities and animal demographics to determine sustainability is still a challenge (Novaro et al. 2000; Siren et al. 2004). In general most hunting occurs near human settlements (Hames 1988; Alvard 1994) and key access points to forests, such as roads or rivers (Begazo & Bodmer 1998; Peres & Lake 2003). Wildlife dispersal may have considerable influence on maintenance of large harvests around settlements through source-sink dynamics (Alvard et al. 1997; Novaro et al. 2000) (i.e., populations with an intrinsic growth rate (λ) > 1 [i.e., sources] that are linked through dispersal to populations with $\lambda < 1$ [i.e., sinks]) (Pulliam 1988). In the hunting literature, the term *sink* often refers to the area around a settlement where hunting offtakes are thought to be augmented by dispersing animals from remote less-hunted or un hunted sources of animals (Novaro et al. 2000; Salas & Kim 2002).

Although there is increasing evidence that there is spatial heterogeneity in hunting effort and offtake over areas hunted by local communities (Van Vliet et al. 2010),

much of the past work on hunting focused on the effect of distance from villages as the main source of heterogeneity in hunting effort and harvest. Studies from multiple tropical forest sites show that hunting pressure decreases as distance from a settlement increases (Alvard 1994; Muchaal & Ngandjui 1999; Siren et al. 2004). Generally, vegetation and other landscape features, such as aquatic areas, topography, or geological features, were not investigated in studies of the distribution of hunting offtake (but see Hill et al. (1997)). When vegetation was studied, researchers focused primarily on the effects of land-cover variation on animal populations, including quantifying hunting effort via surrogate measures of use such as incidence of paths and shotgun shells (Hill et al. 1997; Laurance et al. 2006). These measures of human presence are less accurate than data on hunter offtake. In addition, research on hunting offtake over different land-cover types often compares primary, or relatively undisturbed, forests with current or former agricultural lands, rather than investigating variation within natural vegetation communities and the effects of this variation on hunting effort and offtake (Naughton-Treves et al. 2003; Gavin 2007; Rist et al. 2009).

We investigated how hunting pressure and offtake differ over space, including between naturally occurring forest types, within the logging concession of Kabo, Congo (2°2'N, 16°5'W). This comparison emerged from a larger study in which we sought to document the spatial pattern of hunting pressure and to study the demography of blue duikers (*Cephalophus monticola*), the most commonly harvested species in the study area and throughout central Africa (Mockrin 2009). Initial discussions with hunters about their preference for the open understory of monodominant *Gilbertiodendron dewevrei* forest led us to hypothesize that vegetation influences where people hunt and their hunting success.

We first documented spatial variation in hunting offtake within the catchment and between vegetation types. We then sought to determine how attributes of a hunting area (vegetation and distance from town) combined with attributes of the hunter and hunting trip (e.g., ethnicity, use of transportation, time of hunting) to affect

Table 1. Species hunted in the Kabo area from July 2006 to March 2007.

<i>Hunted species</i>	<i>Number of animals hunted</i>	<i>Percentage of total hunted</i>	<i>Biomass (kg)^a</i>	<i>Percentage of total biomass</i>
Focal species				
Peters' duiker	1101	20.66	17,010	30.48
bay duiker	139	2.61	2,168	3.89
blue duiker	1732	32.51	7,261	13.01
yellow-backed duiker	110	2.06	5,610	10.05
red river hog	230	4.32	13,800	24.73
brush-tailed porcupine	174	3.27	365	0.65
subtotal	3486	65.43	46,216	82.81
Other hunted species				
other rodent species	1	0.02	0.09	0
other ungulate spp.	80	1.50	2,536	4.54
pangolin spp.	7	0.13	148	0.27
primate spp.	1431	26.86	5,904	10.58
reptile spp.	85	1.60	384	0.69
bird spp.	134	2.52	113	0.20
carnivore spp.	104	1.95	505	0.91
Grand total	5328	100	55,806	100

^aTaken from the literature.

hunting activity: the zone selected for hunting, what type of forest animals were harvested in, species composition of harvest by forest type, and the productivity of hunting (biomass harvested/effort). Hunters in Kabo harvested a wide range of vertebrates, but we examined only the most frequently harvested ungulates and one rodent (brush-tailed porcupine (*Atherus africanus*)) because these animals were over 80% of harvested biomass (Table 1) and are most resilient to hunting mortality because their reproductive rates are relatively high (Bodmer et al. 1997).

Study Area

The Kabo logging concession (2960 km²) is south of Nouabalé-Ndoki National Park in northern Congo, a species-rich landscape valued for its populations of large mammals, including great apes and forest elephants (*Loxodonta cyclotis*) (Clark et al. 2009). Kabo is the largest town in the concession, and its population has increased 9-fold to 2600 people as logging has expanded since the 1970s. Ethnic diversity is high in Kabo, with more than 50 ethnic groups present, but ethnicities are commonly grouped into two broad categories: Bantus (farmers and fishers) and BaAka (hunter gatherers). Hunting management responsibilities are held by a cooperative project between the Congolaise Industrielle des Bois logging company, the Wildlife Conservation Society, and the Congolese Ministry of Forestry and Environment (Poulsen et al. 2007). Research and education activities focus on rural livelihoods and consumption of wild animals, and paid personnel enforce hunting regulations. Hunting regulations allow only the use of shotguns and traditional

weapons (wire snares are banned), restrict shotgun hunting to a hunting season from May to October, and prohibit the transportation of hunters and dead animals on logging trucks. There were no informal or traditional restrictions on hunting and traditional hunting weapons are no longer commonly used.

The hunting catchment is 66% Sterculiaceae-Ulmaceae semideciduous forest (hereafter, mixed forest), 28% monodominant forest along water courses and uplands, and 6% *Raphia* spp. swamp (LaPorte 2003). Annual rainfall is 1422 mm, with two peaks, one in May–June and the other in October. There is a short dry season in July and a longer dry season in December–February (CIB 2006). Forest terrain is generally flat, and the region's soils are largely sandy and of low quality for agriculture.

Monodominant forest is widespread across central Africa and is characterized by a sparse understory and 30–40 m *G. dewevrei* trees with deep and narrow canopies (Hart 2001b). Seventy-five percent of stems are *G. dewevrei* and mast fruiting events occur every 2–3 years. Although monodominant forest is 28% of the hunting catchment, discussions with hunters revealed that this forest is valued for its open understory because it allows users to create paths easily. This forest provides little food for vertebrates (Hart 2001b), except in mast years, when *G. dewevrei* seeds are abundant (Blake & Fay 1997). No mast events occurred during this study period. Because sources of food are limited, monodominant forests in the Democratic Republic of Congo (DRC) have half the ungulate biomass of mixed forests (Hart 2001b) and lower primate densities (Thomas 1991). Although similar studies have not been conducted in the Kabo concession, we expected mammal densities between the two forest types to be similar here. The ungulate community in Kabo concession is nearly identical to that of the DRC.

We drew on behavioral and ecological literature to interpret our estimates of hunting offtakes duikers, the most commonly hunted species (Fa & Brown 2009). It is difficult to census duikers, so density estimates vary widely, which complicates efforts to understand the effect of harvest on populations (van Vliet & Nasi 2008). Researchers estimate the following ranges for hunted and unhunted duiker densities: blue duiker 30–78 animals/km², Peters' duiker (*C. callipygus*) 1–16 animals/km², and bay duiker 2–9 animals/km² (*C. dorsalis*) (as summarized by Noss 2000). Duikers disperse short distances (1–2 km) from their natal territory at sexual maturity and then live as adults in small home ranges with stable boundaries (Dubost 1980; Feer 1988; Hart 2001a). In the Kabo concession, only the blue duiker has been the subject of a behavioral study, which established that adult blue duikers' home ranges in mixed forest are 5.8 ha (Mockrin 2009). This finding is consistent with findings in other studies in central Africa. Results of previous studies show that Peters' duiker and bay duiker have larger home ranges of approximately 40 ha (Feer 1988).

Within the Kabo concession, areas used for hunting were all logged selectively for mahogany (*Entandrophragma* spp.) from 1968 to 1988 (≤ 2.5 trees/ha were removed). No clear effects of selective logging on duiker distributions have been documented, whereas hunting substantially reduces duiker densities (White 1994; Laurance et al. 2006; Van Vliet & Nasi 2008). Results of a study in mixed forest in Kabo show that increases in duiker abundance associated with changes in vegetation are countered by increases in hunting where village populations are ≥ 1000 people (Clark et al. 2009). On the basis of these findings and because offtake of ungulates in Kabo is high, we assumed hunting had a major effect on duiker demography.

Methods

A local research assistant conducted interviews with hunters from June 2006 to March 2007. The study period was divided equally between wet and dry seasons. Half the study took place when shotgun hunting was allowed (May–October) and half when shotgun hunting was not allowed (November–April). Hunters continued to hunt during the closed season and to participate in research, although they generally showed increased wariness about enforcement. We conducted interviews only for hunts conducted with shotguns because shotgun hunting was the dominant method of hunting. Snare hunting occurred at low levels, with 10% of all ungulates sold at markets killed by snares (M.H.M., unpublished data). Because snare hunting is prohibited it was not possible to include this type of hunting in our study.

Hunter Interviews

Most interviews occurred within 3 days after a hunt, and we did not include information on any hunt that occurred more than a week prior to an interview. Participation in interviews was voluntary, and we maintained a diverse group of participants, including infrequent and frequent hunters, people native to the Kabo region and immigrants, and Bantus and BaAka. On occasion, hunters were given token gifts, such as a beverage, to thank them for their participation. In each interview, hunters were asked the area where they hunted (areas all had local place names); number of whole or half days or nights they hunted; number of shotgun cartridges taken on each trip, number of shots fired and whether animals were killed, wounded, and missed; and in what type of vegetation animals were shot—mixed, monodominant, or swamp forest. Hunters readily distinguished these vegetation types.

Identification of Hunting Zones

We used local place names for hunting areas to divide the hunting catchment into 11 hunting zones (on average 46 km²) (Supporting Information). Working with residents, researchers mapped each zone in ArcGIS 9 (ESRI, Redlands, California). We excluded a 250 m buffer area on either side of logging roads and a 2 km buffer around the center of the town of Kabo because residents indicated they did not hunt in these areas. We used land-cover data derived from remotely sensed images (Landsat TM) to calculate the area of each forest type (mixed forest, monodominant forest, and “other,” which was mostly swamp) within individual hunting zones (Laporte 2003). Within hunting zones, monodominant forest cover was on average 11.93 km² (SD 6.44) and was surrounded by mixed forest (average 38.09 km² [SD 14.85]) (Supporting Information). Land-cover data were ground-truthed and were accurate when checked during our field research on duikers.

Calculating Offtake

We combined information on species from hunters with weights from the literature to estimate the total biomass harvested. We calculated biomass by scaling each animal's mass by 0.75 to account for age variation within the population (Feer 1993). We used information from interviews to calculate annual harvest rates (animals killed per square kilometer) over three nested spatial extents: hunting catchment (506 km²), hunting zone (average 46 km²), and mixed and monodominant forest areas within each hunting zone (average 31 km² and 13 km², respectively). Annual hunting offtakes were extrapolated from 9 months of data on hunter kills. For each level of analysis (hunting catchment, zone, vegetation within a zone), we divided the number of animals killed by area considered to calculate offtake per unit area. Although hunters likely

did not distribute offtake evenly over zones or forest types within zones, without more specific information on the location of offtake, it was more conservative to include the entire area in estimates of offtake. To verify that it was appropriate to use the hunting zone and vegetation within the zone for offtake analysis, we examined vegetation composition between the more accessible (assumed as within 2.5 km of road) and remote (farther than 2.5 km from road) parts of a hunting zone. Ratio of area of monodominant to mixed forest within the 2.5 km buffer and within the entire zone were highly correlated ($r = 0.82$, $df = 10$, $p = 0.002$), demonstrating that the zone's vegetation composition did not differ in the accessible and remote portions of each hunting zone.

Statistical Analyses

Approximately 90% of hunting trips took place in the Kabo concession, Congo, with 10% of hunts occurring across the Sangha River in Cameroon. Because we had no data on vegetation cover for Cameroon and not many animals were taken from this area, we excluded these trips from our analyses. We focused our analyses on determining how features of the hunting zone (vegetation, distance), the hunter, and the hunting trip determined the distribution of hunting effort (measured as trips). To determine the relation between vegetation composition and hunting effort, we related the number of hunting trips in a zone to each zone's vegetation composition (ratio of monodominant forest to mixed forest) and a zone's distance from town. For all analyses, we measured distance from town as the linear distance from the center of town to the middle of the zone. We selected this distance measure by examining three other measures of distance in the analysis of hunting offtake (discussed below) and selecting the measure that minimized Akaike's information criterion (AIC). Alternative distance measures were the straight-line distance from the town to the closest point of the hunting zone, the distance along the road to an access point for each zone, and the distance along the road plus the straight-line distance to the center of the zone.

Hunters may differ in their behavior, so we examined the distribution of hunting trips with the individual hunter as the unit of analysis. We used the proportion of each individual's hunts in areas with relatively little monodominant forest as the response variable and ethnicity as a covariate in linear models for each of the following binary variables: distance of hunting zones to the town (near or far), time of hunting (day or night), season (dry or wet), transportation during the hunt (on foot or with a vehicle [truck, bicycle, or motorcycle]). We weighted these models by the log of the total number of hunting trips+1 for each hunter to avoid biasing results by frequency that an individual hunted. Distance and vegetation composition were divided into two groups on the

basis of divisions within the data series (distance: near [7–11 km, $n = 6$] or far [16–25 km, $n = 5$]; vegetation: low [0.22–0.34, $n = 6$] or high ratio of monodominant to mixed forest [0.39–0.95, $n = 5$]). Although this approach required attributing categorical values to landscape features for hunting zones, it allowed us to examine the behavior of individual hunters, many of whom were interviewed more than once and thus were repeated measures, relative to features of interest in the hunting trip and the area hunted.

We then examined how the productivity of the hunting trip, measured in several different ways, related to features of the zone hunted, the hunting trip, and the individual hunter. We first examined productivity of the hunting trip in terms of shots fired and animals killed in relation to vegetation distribution. If animals were harvested evenly across land-cover types, we expected shots fired or animals killed per unit area to be equally distributed between vegetation types. We used linear regression to relate the proportion of animals shot and harvested in monodominant and mixed forest to the land-cover composition of each hunting zone. We also examined species composition of harvested animals within each forest type to determine whether hunters were more likely to obtain heavier, more desirable species in different forest types. We compared the contribution of two species (blue duiker, red river hog) and three species groups (primate, medium-sized duikers [Peters', bay, white-fronted *C. leucogaster*, or black-fronted *C. nigrifrons*], and other animals) to the harvest in each forest type with a *G* test. For this analysis, we excluded all animals killed in the other forest category because they comprised 130 of 5312 animals in our data (mostly red river hogs killed in swamps).

We then investigated the relation between biomass harvested over time and characteristics of the hunting zone, hunter, and the hunting trip. For the analysis of biomass harvested, we restricted the data set to only those hunts that were 1 day or 1 night ($n = 1269$) to control for effort. We conducted a maximum likelihood analysis in which total biomass harvested per trip was the response variable and the general linear mixed models were fitted and evaluated with a log-link function with the Laplace approximation (lme4 package in R) (Bolker et al. 2009) (R version 2.9, R Development Core Team 2009). Hunter's ethnicity and characteristics of the hunting trip (number of cartridges taken, time when hunting occurred, transportation, and features of the hunting zone [distance from town, vegetation]) were fixed factors. After exploratory analysis, we included interactions between the number of cartridges taken and the hunter's ethnicity and the time of hunting. Because individual hunters were interviewed repeatedly, we incorporated hunter as a random effect, as an intercept and as a slope, and used month as a random effect to investigate changes over time. To select the best model fit, we tested different random effects with a full model of fixed effects. We used AIC

and a Δ AIC threshold of two to compare models (Burnham & Anderson 2002). When comparing random effects models, all fixed effects were included and models were fitted with restricted maximum likelihood. After selecting random effects, we reduced the fixed-effect structure. We tested the statistical significance of individual fixed effects with F statistics and report the effect size of model parameters.

Results

Hunters reported harvesting 5328 animals (55,806 kg) in 1561 hunting trips with 147 hunters (Table 1). There was wide variation in the number of trips reported by individuals (median hunts per subject = 16, \bar{x} [SD] = 41 [61]) because hunting is only one of the activities people pursue to earn their livelihoods.

Use of Hunting Zones

The number of visits to a given zone varied considerably (Fig. 1). The number of visits was inversely related to the ratio of monodominant to mixed forest ($F = 12.1$, $R^2 = 0.57$, $p = 0.007$, $df = 10$) (Fig. 1). Hunters visited zones with low proportions of monodominant forest most frequently and rarely visited zones with high proportions of monodominant forest. Distance between the town and hunting zones was not significantly related to the number of visits ($F = 0.32$, $R^2 = 0.03$, $p = 0.59$, $df = 10$) (Fig. 1). When examining individuals' patterns of hunting activity over time there were no statistically significant differences between BaAka and Bantu hunters' use of hunting zones, so we present estimates for the entire population (Fig. 2). An average 83–90% of hunting visits made by individual hunters on foot (1178 hunts) were to zones with relatively low proportions of monodominant forest (Fig. 2). When analyses were conducted separately for wet and dry seasons, most visits again were to areas with low amounts of monodominant forest. The proportion of visits to these zones was lowest in the dry season for hunts conducted farther from town. Most visits conducted with vehicles ($n = 180$) were to areas with relatively little monodominant forest, although the association was less marked for hunts close to town during the day than those far away or those close to town at night. Sample size for hunts conducted with vehicles was too small to allow subdivision of the data set by season.

Species Harvested and Forest Types

Although hunters visited areas with small amounts of monodominant forest most often, they consistently reported shooting a high proportion of animals in monodominant forest (\bar{x} [SD] = 0.67 [0.07], $n = 12$). The proportion of shots fired and biomass harvested in mon-

odominant forest was not related to vegetation composition of the zone (shots fired: $F = 0.105$, $R^2 = 0.01$, $p = 0.75$, $df = 11$; biomass harvested: $F = 0.33$, $R^2 = 0.04$, $p = 0.58$, $df = 11$). Species' prevalence in offtake differed between monodominant and mixed forest ($G = 26.21$, $p < 0.0001$, $df = 4$). Less profitable (smaller) species, such as blue duikers and primates, were killed more frequently in monodominant forest than in mixed forest. Blue duikers and primates made up larger proportions of the harvest in monodominant forest than in mixed forest (blue duikers: 33% of harvest in monodominant forest, 26% in mixed forest; primates: 29% in monodominant and 26% in mixed). Red duikers, red river hogs, and other animals were more commonly killed in mixed forest than in monodominant forest (red duikers: 24% monodominant, 30% mixed; red river hogs: 2% monodominant, 4% mixed; other: 11% monodominant, 14% mixed).

Hunting Offtake

The most parsimonious model included hunter as a random effect, both as an intercept and as a slope with number of cartridges, which indicated hunting offtake varied among hunters and that individuals' relations between offtake and number of cartridges varied (Table 2). Fixed effects that influenced productivity of a hunting trip included the number of cartridges plus the quadratic form of number of cartridges, hunter ethnicity, interaction between ethnicity and number of cartridges, time of hunting, transportation used by hunters, amount of monodominant forest relative to mixed forest, and a zone's distance from town (Tables 2, 3). Including the number of helpers and an interaction between time of day and number of cartridges resulted in a change of <2 AIC and the p values for these variables were not significant. In general, hunting at night yielded more offtake, as did hunting with a truck, bicycle, or motorcycle. Bantu hunters harvested more biomass than BaAka hunters. More cartridges resulted in higher biomass harvested, but harvest decreased as the number of cartridges continued to increase (indicated by the inclusion of the quadratic form of number of cartridges). Harvest biomass increased slightly as distance from town and vegetation ratio of monodominant to mixed forest increased, but effect sizes were minimal.

Offtake and Spatial Scale

Variation in offtake by hunting catchment, hunting zone, and vegetation type within hunting zones was similar to the unequal distribution of hunting offtake described above. At the level of hunting zones, hunters concentrated effort in areas close to town with little monodominant forest and killed many animals (Fig. 3). Because offtake in monodominant forest was much higher than offtake in mixed forest in all hunting zones, those zones with a low proportion of monodominant forest with the

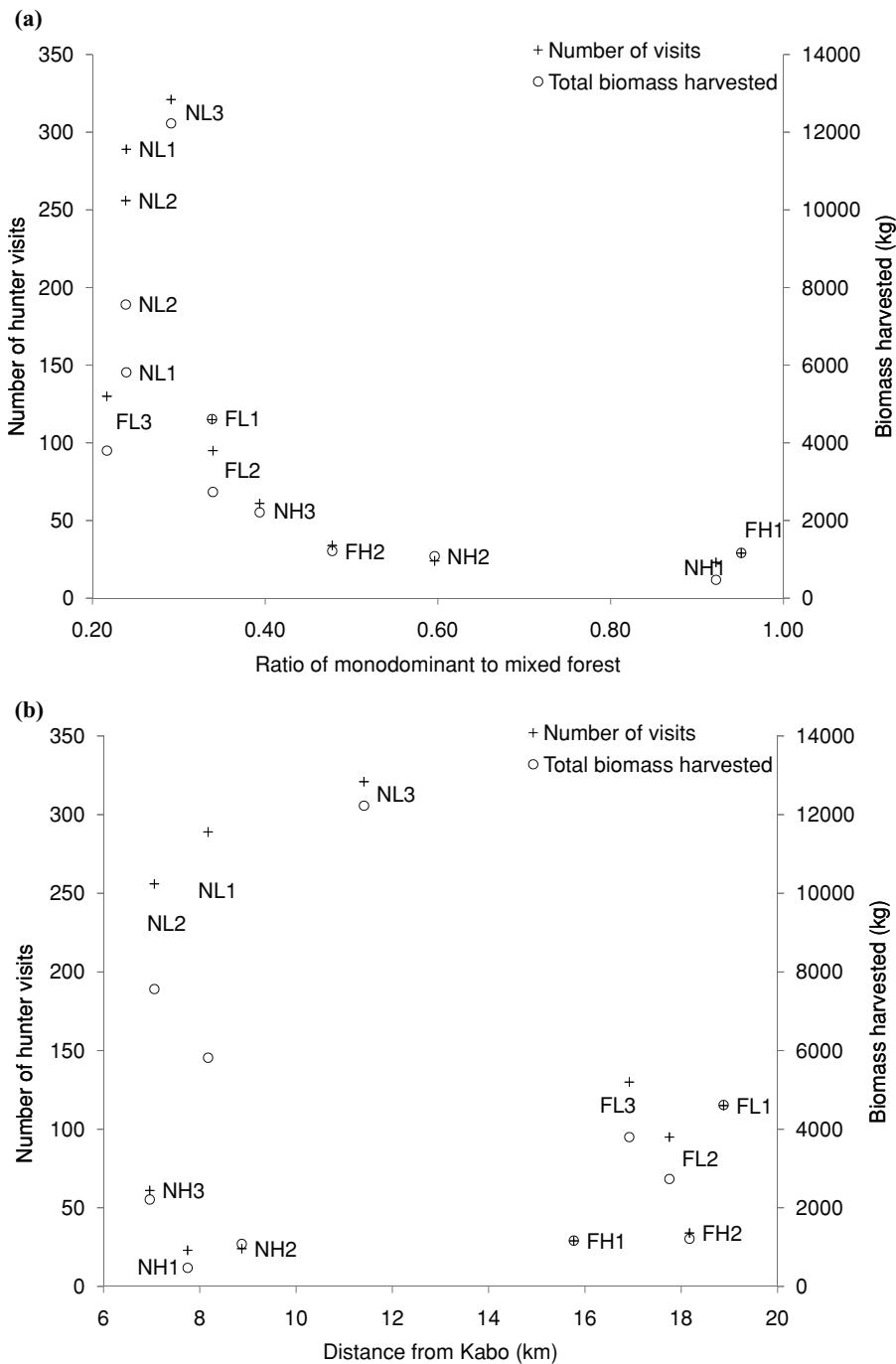


Figure 1. Relation between the number of hunter visits to and biomass harvested from a hunting zone and the (a) vegetation composition of the area and (b) distance from town. Zones are labeled with a combination of their distance (N, near; F, far) from town and vegetation as measured as proportion of monodominant relative to mixed forest (L, low; H, high).

most visits also had the highest harvests from within monodominant forest. Measured at the extent of hunting catchment, harvests were much smaller. Offtake of red river hogs was highest in the other forest category because these animals associate with swamp forest.

Discussion

Understanding the spatial distribution of hunting pressure and its effects on wildlife population dynamics is nec-

essary to assess hunting sustainability. In the Kabo concession, the spatial distribution of offtake was strongly associated with vegetation, both within and between hunting zones. Within individual hunting zones, hunters obtained most of their harvest in monodominant forest. Hunters stated consistently that limited undergrowth in monodominant forest allowed them to easily establish paths and campsites and increased visibility for shotgun hunting.

Assessing the effects of variation in hunting intensity among vegetation types on prey population demography

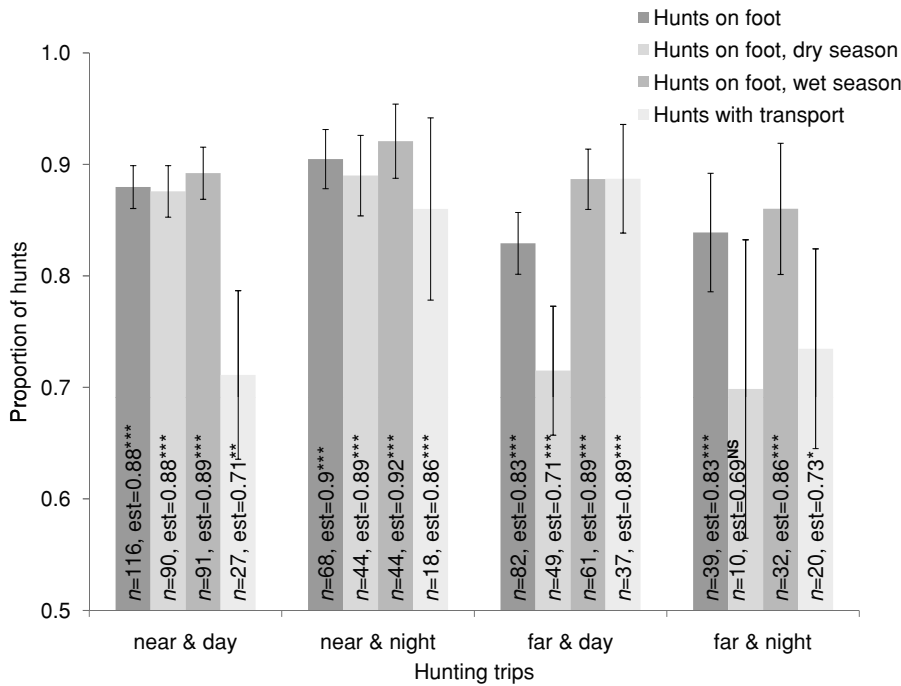


Figure 2. Means and 95% CI for proportion of hunting trips in areas with low proportions of monodominant forest for different combinations of an zone's distance from town (near, far) and time of the hunt (day, night). Estimates (est) are averages of individual hunters' pattern of activity in four different categories (n, number of individual hunters in each subset; p values based on expected value of 0.50 if no difference in visitation with vegetation types; ***p < 0.001, **p < 0.001, *p<0.05).

is challenging. There are several methods for estimating maximum sustainable offtake of duikers on the basis of life-history parameters (e.g., Robinson & Redford 1991). These estimates of sustainable harvest vary widely due to differences in estimates of duiker densities and reproduction (van Vliet & Nasi 2008), and these estimates are not designed for use when harvest levels differ in space (Fa

& Brown 2009). Nevertheless, in Kabo, the high levels of offtake in monodominant forest, current knowledge of duiker reproduction and densities, and the low productivity of mammals in monodominant forest suggest that local reproduction within this forest type is unlikely to sustain these levels of harvest. For example, if past results on the differences in blue duiker densities between

Table 2. Comparisons for models of hunting offtake (biomass per unit effort) that included the number of cartridges (cart), ethnicity^a (eth), time of hunting, number of helpers^b (help), transportation^c, distance from town (dist), and ratio of monodominant to mixed forest (veg).

Model	df	AIC	ΔAIC	Weight
Random effects (effect by grouping variable) ^d				
cart by hunter	16	3369.7	0.0	0.75
cart+cart ² by hunter	19	3372.0	2.4	0.23
1 by hunter	14	3376.5	6.8	0.03
1 by month	14	3415.5	45.9	< 0.001
Fixed effects ^e				
full model (eth+cart+cart ² + time of hunting+ help + transport + dist + veg + cart*eth + cart*time of hunting)	16	3311.8	0.0	0.30
-help	14	3312.3	0.5	0.24
-cart*time of hunting	15	3312.5	0.7	0.21
-veg	15	3314.5	2.7	0.08
-transport	15	3314.5	2.7	0.08
-dist	15	3314.6	2.8	0.08
-time of hunting	15	3318.8	7.0	0.01
-eth	15	3326.9	15.1	< 0.001
-cart*eth	15	3327.6	15.8	< 0.001

^aBantu or BaAka.

^bTreated as a factor.

^cEither on foot or with a vehicle.

^dRandom effects noted in the form of effect by grouping variables. For example, cart by hunter indicates a random slope for cart and a random intercept for each hunter, whereas a 1 indicates that only a random intercept was fitted.

^eFixed-effect models are written as subtractions from the full model. For example, -help is the full model without the variable for number of helpers.

Table 3. Parameter estimates for a mixed-effects model of hunting offtake biomass.

Variables ^a	Estimate	SE	F	p ^b
Intercept	1.5	0.252		
Eth(BaAka) ^c (baseline Bantu)	-0.821	0.196	7.175	0.008
Cart	0.337	0.058	278.16	0.00
Cart ²	-0.014	0.004	51.86	4.1 × 10 ⁻¹¹
Time of hunting (night) (baseline day)	0.694	0.231	22.60	5.2 × 10 ⁻⁶
Help(1) factor (baseline 0)	0.203	0.100	0.912	0.40 (for overall F test, df = 2)
Help(2+) factor	0.137	0.129		
Trans(foot) (baseline transport)	-0.177	0.081	8.89	0.003
Dist	0.013	0.006	6.23	0.02
Veg	0.381	0.176	4.83	0.03
Eth(BaAka)*cart	0.122	0.027	19.88	1.7 × 10 ⁻⁵
Time(night)*cart	-0.057	0.034	2.72	0.10
Random effects ^d				
Hunter (intercept)	0.597			
Cart by hunter	0.059			

^aVariables include the number of cartridges (cart), ethnicity (eth; either Bantu or BaAka), time of hunting (day or night), number of helpers (help), transport (on foot or with a vehicle), distance from town (dist), and ratio of monodominant to mixed forest (veg).

^bData set consisted of 1269 hunting trips made over 133 hunters so a df = 132 was used to calculate p values.

^cEffects for categorical variables are contrasts relative to the first categorical level with an estimate set at zero. First categorical levels are listed below contrasts.

^dEstimate for the random effect of cartridge by hunter is the SD, a measure of the variance in offtake per hunter.

mixed and monodominant forest are consistent here, one could expect the highest density in un hunted monodominant forest to be 34 blue duikers/km² (half of the highest estimate of blue duiker density for mixed forest in Gabon (Dubost 1980). In zones close to town, hunters reported harvesting up to 35 blue duikers/km²/year in monodominant forests, an area where hunters have used shotguns for 30 years. We suggest that these large harvests in monodominant forests may be sustained in part by dispersal of duikers from mixed forest into monodominant forest.

Simulations of hunting-created source-sink dynamics predict that the greatest offtake will occur where small areas of high hunting pressure can draw on larger "sources" of animals with low or no hunting (McCullough 1996; Salas & Kim 2002; Siren et al. 2004). By concentrating offtake in small patches of monodominant forests surrounded by larger areas of mixed forest, hunters in Kabo may be targeting those areas that are both accessible and productive. Unlike results of previous studies, our results show distance from the town was not the strongest association with use of an area for hunting; hunters were willing to travel farther to reach zones where there was relatively little monodominant forest. Data on vertebrate offtake collected in Kabo markets from 1999 to 2000 showed the same distribution of hunting activity (M. Eaton, unpublished data), indicating that this association has been stable over time. We found no clear relation between hunting productivity and a hunting zone's distance from town or type of vegetation, although our estimates of time spent hunting were relatively coarse, restricted to the number of whole or half days or nights. Even with more information on the spatial and tempo-

ral distribution of hunting offtake, the lack of information on prey population demography in different vegetation types, other sources of temporal and spatial heterogeneity, and hunters' time allocation while hunting may restrict efforts to understand the role of hunting in population dynamics and sustainability of offtake (Van Vliet et al. 2010). Although understanding the effects of heterogeneity in hunting pressure may therefore remain challenging, such variation in hunting offtake over space is likely to be common in central Africa and elsewhere. Monodominant forests are widespread throughout central Africa (Hart 2001b), and duikers are the most heavily harvested species in the region, which suggests the high harvests in monodominant forest observed in Kabo may occur in other areas with shotgun hunting. In addition, in both tropical and temperate settings, there is growing evidence that hunters concentrate their efforts around paths (Alvard 1994; Broseth & Pedersen 2000; Stedman et al. 2004; Rist et al. 2009).

Recognizing such localized variation in hunting pressure will reframe the concept of hunting-induced source-sink dynamics. In the past, researchers often documented heavy hunting pressure in areas near settlements, and it was suggested that high levels of offtake in these areas were sustained by dispersal of animals from more remote, less-hunted areas outside the catchment. Nevertheless, for animals that are not highly mobile (such as duikers), shorter dispersal events, in response to localized hunting pressure (e.g., around paths) that creates vacant home ranges, are more realistic than long-distance dispersal from outside a hunting catchment. Other species will respond differently to hunting. For example, primates (27% of the individual animals killed in Kabo) are

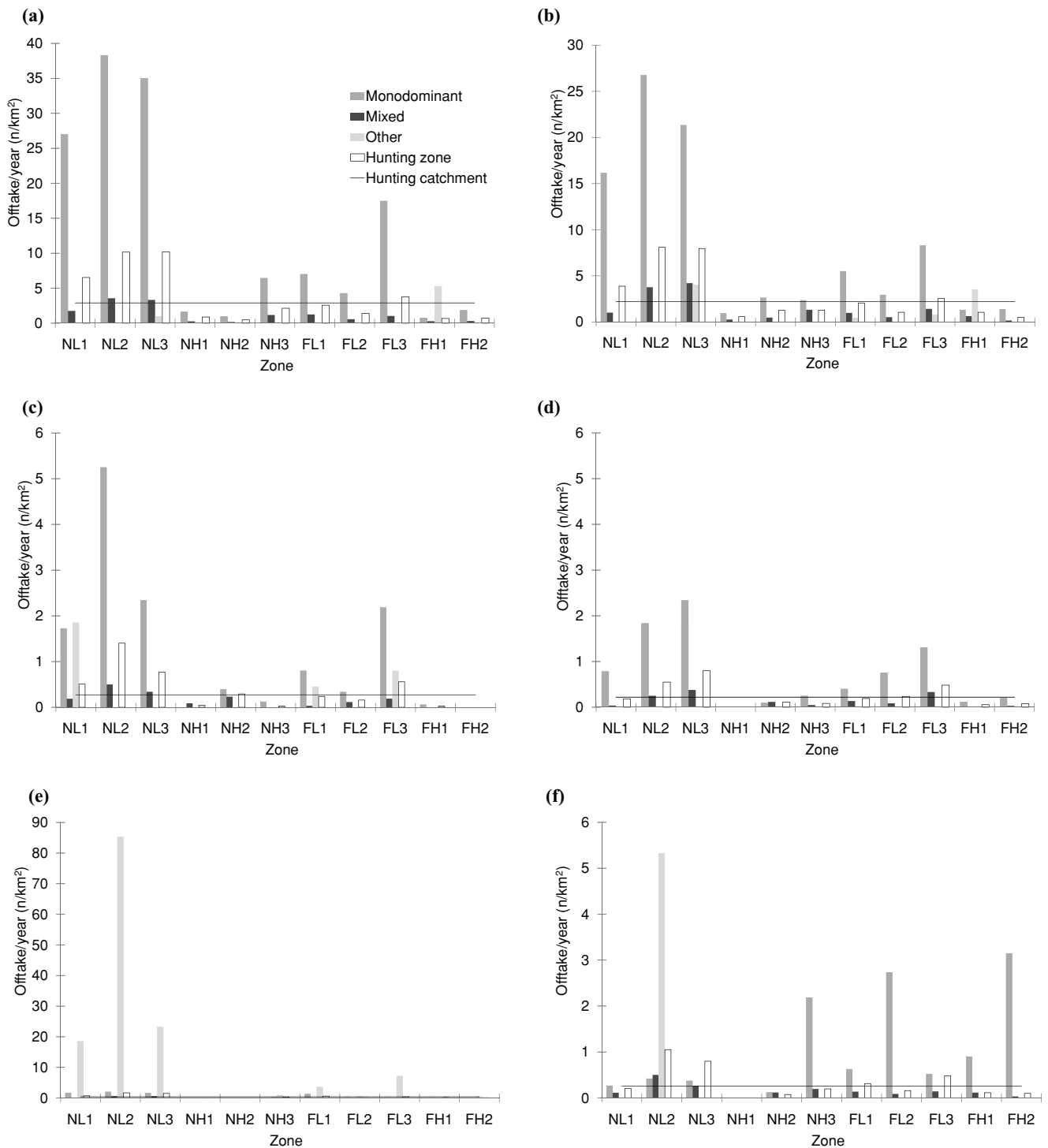


Figure 3. Hunting offtake over three spatial extents (hunting catchment, hunting area, and forest type [monodominant, mixed, other] within hunting area) for (a) blue duiker, (b) Peters' duiker, (c) bay duiker, (d) yellow-backed duiker, (e) red river bog, and (f) brush-tailed porcupine (N, near village; F, far from village; L, low or H, high, ratio of monodominant to mixed forest).

unlikely to exhibit source-sink dynamics because of their complex social structures and low productivity.

Some managers would like to establish no-take zones on the basis of source-sink dynamics to ensure sustain-

able hunting of wild animals. No-take areas would thus serve as sources for dispersing animals and refuges for resident animals. The existence of fine-grained distribution of hunting offtake in Kabo implies that creating large

no-take zones outside hunting catchments (e.g., Novaro et al. 2000) may not supply large numbers of dispersing animals. In Kabo several such no-hunting zones have been established outside of areas commonly used for hunting. Although these large and remote source areas are easy to delineate and enforce and are likely effective in protecting resident animals, simulations suggest that multiple no-take zones intermixed with hunting areas will lead to higher dispersal and offtake (Salas & Kim 2002). If duiker hunting offtakes in monodominant forest in Kabo are enhanced by dispersal from mixed forests, establishing no-take zones in mixed forests within actively hunted zones may make a greater contribution to sustainable harvest by allowing the dispersal of animals that can be harvested. This restriction may be relatively well received by local populations because they would not involve restrictions on hunting where offtake is currently the highest (i.e., monodominant forest). Although multiple source areas may promote dispersal, no-take zones cannot ensure hunting will be sustainable. The sustainability of offtake depends on the distribution and intensity of hunting (including no-take zones) and the demography of hunted species.

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Supporting Information

A map of the Kabo hunting catchment showing vegetation composition and hunting areas is available online (Appendix S1). The authors are solely responsible for the content and functionality of these materials. Queries (other than the absence of the material) should be directed to the corresponding author.

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