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Edge effects and large mammal distributions in a national park

C. Kiffner[1], C. Stoner[2] & T. Caro[1,3]

1 Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA, USA
2 Environmental Science, Policy, and Management, University of California, Berkeley, CA, USA
3 Tanzania Wildlife Research Institute, P.O. Box 661, Arusha, Tanzania

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Correspondence
Christian Kiffner, University of California, Wildlife, Fish, and Conservation Biology, 1 Shields Avenue, Davis, CA 95616, USA.
Email: cfkiffner@ucdavis.edu

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Abstract

While protected areas are a centrepiece of conservation, populations of animals in protected areas can still be subject to considerable human influence. Conservation theory suggests that many species should live at lower densities at the periphery of protected areas compared with the core area. Similarly, but more specifically, species subject to exploitation are expected to have lower densities in areas close to human settlements compared with more remote areas. Drawing upon distributional data of eight large African herbivore species (buffalo *Syncerus caffer*, elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, impala *Aepyceros melampus*, topi *Damaliscus lunatus*, warthog *Phacochoerus africanus*, waterbuck *Kobus ellipsiprymnus* and zebra *Equus quagga*) sampled using ground surveys in 1995 and 1996, and seven large herbivore species (the same species without impala) sampled using aerial surveys from 1987 to 2009, we fitted logistic regression models and used an information theoretic model selection approach to test these two hypotheses in an East African savannah national park subject to illegal hunting from outside. In the vast majority of herbivore species, occupancy was not substantially affected by being close to the edge of the park or in close proximity to human villages. Furthermore, population declines witnessed in this protected area were not reflected in reduced occupancy near park boundaries. We conclude that assumed distributional differences between peripheral and core parts of reserves are not necessarily supported by empirical evidence, and that population declines within reserves do not inevitably proceed from boundaries inwards.

Introduction

Protected areas are the backbone of conservation and are intended to be safe havens for the species' inhabiting them, but it is well recognized that many protected areas do not function very effectively (e.g. Caro & Scholte, 2007; Stoner *et al.*, 2007*a*; Western, Russel & Cuthill, 2009; Craigie *et al.*, 2010). Unfortunately, we do not yet understand changes in species distributions, declines in abundances or species losses that occur within protected areas, or the mechanisms that cause these ecological changes (Chape *et al.*, 2005; Gaston *et al.*, 2006), although conservation theory does predict that losses will be greatest in small reserves (Diamond, 1975) and in reserves surrounded by high human densities (Woodroffe, 2000; Parks & Harcourt, 2002).

Inside reserves, effective protection is likely to vary by location because of abiotic factors and numerous indirect and direct human activities that often occur immediately outside and just inside reserve borders, such as firewood collection, cattle grazing, bush fires, fishing and hunting, that can affect plants and animals living inside the periphery of the reserve (Laurance, 2010). Protection of peripheral portions of reserves is one of the reasons for placing buffer zones around reserves, as advocated by the United Nations Educational, Scientific and Cultural Organization's Man and the Biosphere Programme (Batisse, 1986), and is formalized in the International Union for Conservation of Nature's protected area categories IV through VI (e.g. Hansen *et al.*, 2011). This sort of edge effect can be termed the core–periphery phenomenon (CPP). In addition, in those reserves delineated to protect dry season concentrations of large mammals (e.g. Caro, 2003), key resources are often in central parts of protected areas, while areas closer to park boundaries may be less attractive to wildlife during dry seasons.

Individuals of species living in a reserve but just within its border, and that are sought after by people, are more likely to be subject to anthropogenic disturbance, and hence are hypothesized to live at lower population densities compared with individuals in the reserve centre, or they may be entirely absent just inside the reserve boundary. In the tropics, for instance, bushmeat hunters enter protected areas from outside but to a decreasing extent with distance from their settlements (Hill *et al.*, 1997; Muchaal & Ngandjui, 1999;

Metzger *et al.*, 2010; Lindsey *et al.*, 2011), and are therefore expected to have greater effects on wildlife in parts of protected areas that are easily accessible to human hunters (Yackulic *et al.*, 2011). This can be termed the local exploitation phenomenon (LEP), which is a more specific version of the CPP. For both these reasons, species exploited by people are predicted to suffer greater mortality at reserve peripheries than at the centre, or in the case of animals, perhaps to actively avoid reserve peripheries, both of which will result in lower densities at reserve margins.

Despite reserve edge effects being part of conservation dogma (e.g. Groom, Meffe & Carroll, 2005; Primack, 2010), the topic has actually received little empirical attention. The most cited studies focus on large carnivore species (Woodroffe & Ginsberg, 1998; see also Revilla, Palomares & Delibes, 2001; Balme, Slotow & Hunter, 2010). These investigations show that large carnivore species that have large individual home ranges that extend beyond reserve boundaries require larger reserves to sustain viable populations. Findings are attributed to human-induced mortality outside reserves, which drains a population within the reserve to a point where it is no longer viable.

To examine the generality of the idea that reserves are spatially heterogeneous in terms of their conservation functionality, here we examine predictions of both the CPP and LEP hypotheses in relation to herbivore distributions within a protected area in East Africa, Katavi National Park. Using occupancy data for several large wildlife species, the CPP hypothesis predicts that occupancy is higher in core areas compared with edge areas of this park. This effect might be more pronounced during the dry season since Katavi National Park was originally gazetted to protect dry season water sources. Given that wildlife populations in the Katavi-Rukwa ecosystem are subject to substantial hunting offtake from local people living to the north and south of the park, the LEP hypothesis predicts that occupancy of wildlife species should be lower in areas close to human settlements. Additionally, we would expect that wildlife populations would decline disproportionately over time in edge areas where they are subject to anthropogenic pressures.

Methods

Study site

Our study site was Katavi National Park (NP) in Rukwa Region of western Tanzania (6°35'–7°05' S, 30°45'–31°25' E). The park was gazetted in 1974, and in 1998 it was extended to the east and south-east and now constitutes the country's third largest NP. We used its pre-1998 extension boundaries; the study area covered an area of 2253 km^2 (Fig. 1a). The area is part of the central Zambezi miombo woodlands ecoregion (Burgess *et al.*, 2004) but, unusually for miombo, is characterized by trees of the *Terminalia* and *Combretum* genera (Banda, Schwartz & Caro, 2006; Banda *et al.*, 2008). A great diversity and abundance of large mammals occur in this area (Caro, 1999*a*,*b*, 2003), which is currently under

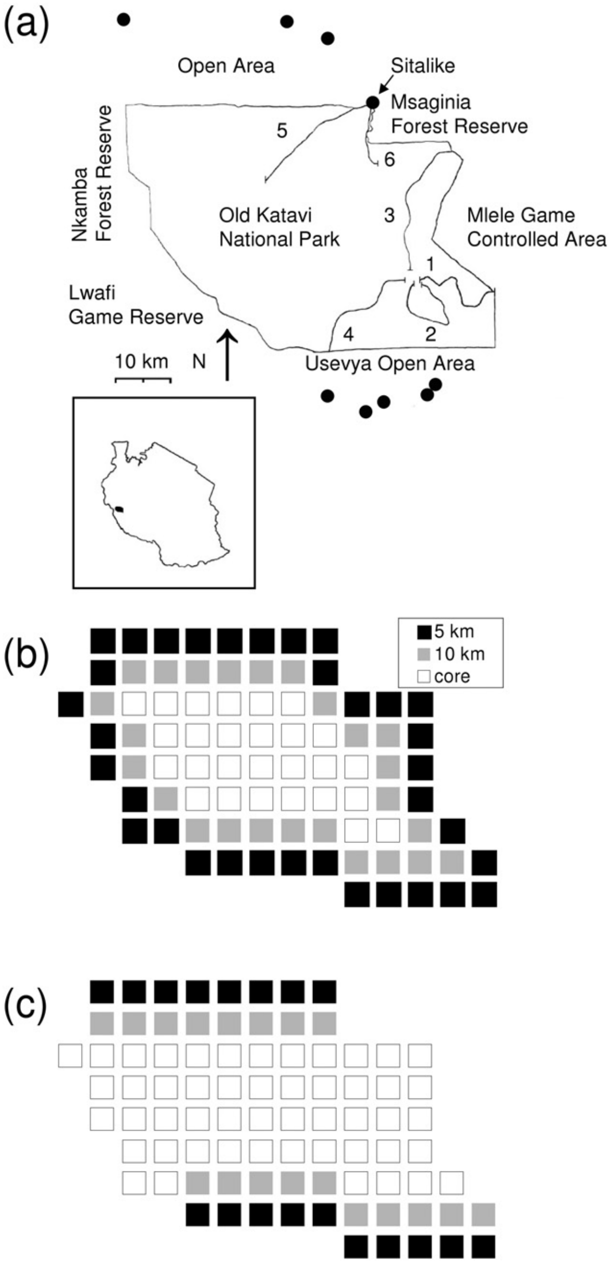

Figure 1 (a) Map of Katavi National Park (original boundaries; the park was later extended to the east in 1998), six numbered ground transects, location of nearest surrounding villages (black dots to the north and south of the park), and the areas surrounding the park. Insert shows the location of Katavi in Tanzania. (b) Map of Katavi National Park showing the location of 5 × 5 km grid squares immediately adjacent to the old park boundary and within 10 km of the boundary (CPP hypothesis). (c) Location of 5 × 5 km grid squares immediately adjacent to the hard boundaries north and south of the park and within 10 km of those boundaries (LEP hypothesis). CPP, core–periphery phenomenon; LEP, local exploitation phenomenon.

several different forms of protection. The dry season lasts from June to November, and the wet season from December to May.

The NP is administered and patrolled by Tanzania National Parks; no settlements or exploitation are allowed within NP boundaries. To the west of the NP lies the Nkamba Forest Reserve, and to the south-west is the Lwafi District Game Reserve. No settlements are allowed in these two areas, but logging and hunting companies operate there. To the north-east is the Msanginia Forest Reserve, where both legal and illegal logging and legal mining and fishing occur but no settlements are allowed. Formerly, to the east of the NP was Mlele Game Controlled Area, where legal logging and hunting occurred but this area achieved NP status in 1998 (Caro, 2011). The western and eastern sides of the NP, therefore, constitute soft boundaries. Additionally, the northerly and southerly boundaries are subject to firewood collection, cattle grazing and fishing expeditions. These anthropogenic activities in the periphery of the well-protected NP therefore provide an opportunity to test predictions of the CPP hypothesis.

To the north of the park there is an open area (*c*. 7000 persons in the ward in 2002) with scattered villages, the most prominent of which is Sitalike, immediately on the NP boundary. To the south of Katavi NP lies Usevya Open Area (*c*. 16 000 people in the ward in 2002); within 12 km of the old park boundary are five villages. It is illegal to hunt animals in open areas without a licence, but in practice, illegal subsistence hunting is widespread (Caro, 2008), so given the proximity of villages, the northern and southern boundaries of the NP constitute areas of human influence and can be thought of as hard boundaries. This provided an opportunity to test spatial predictions raised by the LEP hypothesis for reserve functionality.

Ground counts to determine presence

We used two methods to examine distributional differences of wildlife species between periphery and core of the NP. Ground surveys were conducted by regularly (almost every month, always between dawn and 10:30 AM) driving six vehicle transects along all the minor tracks in Katavi NP at that time (Fig. 1a) between September 1995 and December 1996 (Caro, 1999*a*). Transects passed through seven different types of woodland and plains habitats (see Caro, 1999*a*). Mammal species were counted on both sides of transects up to an estimated distance of 500 m; species were relatively tame and rarely fled from vehicles. For analyses, we considered only species that are easily detected, and for which we had > 100 independent sightings: elephant *Loxodonta africana* ($n = 114$ sightings), giraffe *Giraffa camelopardalis* ($n = 238$), buffalo *Syncerus caffer* ($n = 254$), zebra *Equus quagga* ($n = 230$), topi *Damaliscus lunatus* ($n = 172$), waterbuck *Kobus ellipsiprymnus* ($n = 296$), warthog *Phacochoerus africanus* ($n = 235$) and impala *Aepyceros melampus* ($n = 118$). We plotted each independent sighting (i.e. herds or groups of one species were considered as one sighting) on a map, and assigned to it the distance to the nearest park boundary (measured in 2-km intervals) and the main habitat type (open habitat vs. woodland). These locations were used as presence data in our distribution models.

Open habitat corresponded to grassland, wooded grassland and bushed grassland; woodland habitat corresponded to three types of woodland and bushland (see Caro, 1999*c*). Using the vehicle transect data, we only tested the CPP hypothesis because there were insufficient transects to the north and south of the NP.

Aerial counts to determine presence

To test both the CPP and the LEP hypotheses, we considered aerial surveys for Katavi National Park available to us. These were dry season surveys 1987, 1991, 1998, 2002, 2006 and 2009, and the wet season surveys 1988, 1995 and 2001 obtained from Serengeti Ecological Monitoring Programme, Tanzania Wildlife Conservation Monitoring Programme and Conservation Information Monitoring Unit reports of repeated systematic reconnaissance flights of an area of *c*. 12 000 km^2 (see Caro, 2011, for references). Such data have been extremely useful in documenting animal population changes over wide areas of Tanzania (Stoner *et al*., 2007*b*). Fixed-wing planes were used for travelling along systematically placed, 5-km spaced transects (Norton-Griffiths, 1978), and animal sightings were plotted on maps at a resolution of 5 × 5 km grid cells. Unfortunately, animal densities per grid cell were reported inconsistently across years, and hence we applied a presence/absence approach (occupied cells = 1, unoccupied cells = 0). Given the coarse spatial resolution of the aerial census data and our two hypotheses, we used two different approaches to define 'edge areas' inside the NP. For testing the CPP hypothesis, we defined lines of grid squares as edge areas (i.e. a band of 10 km within the park), and in a second approach, we defined only the outermost line of grid squares as edge area (i.e. a band of 5 km within the park) (Fig. 1b). In order to test the LEP hypothesis, we compared only those 5 × 5 km grid squares that lay adjacent to just the northern and southern boundaries of the NP close to villages with all other grid squares in the NP (Fig. 1c); in the east and west, Katavi borders other protected areas, so human encroachment is unlikely to come from these directions. We examined presence/absence of the eight species counted from the air in grid squares along two bands (10 km in) because that is the distance that people can easily walk into the NP, and along the 5 km band as this is where the effects of human disturbance might be strongest.

We classified every grid square in the NP as either predominantly open habitat (usually floodplain) or wooded habitat (miombo woodland) by superimposing the grid squares over a vegetation map. We included data for elephant ($n = 26$ presences during all aerial surveys), giraffe ($n = 38$), buffalo ($n = 61$), zebra ($n = 53$), topi ($n = 43$), warthog ($n = 39$) and waterbuck ($n = 24$); impala ($n = 10$) were rarely detected and were not included in these analyses. For each species, we fitted separate models; to allow comparisons with a previous study (Kiffner *et al*., 2009), we also fitted models for all of our mammal species (wildlife) combined. This was only done for the ground vehicle data, however, because distributional data of certain species were missing in some of the aerial data reports and only two years contained distributional data of all species.

Statistical analyses and model selection

In order to model the distribution of animals counted from vehicle transects, we required additional data representing the range of environmental conditions (habitat type, distance to park boundary) in the covered region. Since we used roads to assess distribution of animals, and hence followed a potentially biased sample selection protocol (roads are not likely to traverse a random suite of environmental gradients in the park), we selected the background data along the same gradient. This procedure is superior than generating random background from the entire area because differences in occurrence and background sampling may lead to biased species distribution models (Philipps *et al.*, 2009). Therefore, we generated pseudo-absences along each transect. Each pseudo-absence was spaced 100 m apart from each other (a total of 1329 pseudo-absences). We fitted mixed-effect generalized linear models with binomial error structure (i.e. logistic regression models) using the 'glmer' function implemented in the *R* package 'lme4' (Bates, Maechler & Dai, 2008; R Development Core Team, 2011), and tested the effect of habitat type and distance to park borders on the likelihood of animal presence; that is, we defined the response variable as presence = 1 (locations where animals were actually sighted) and pseudo absence = 0 (the suite of environmental variables after each 100 m of transect). To account for the nested sampling approach, we included the transect ID as a random effect; transects usually crossed both open and woodland habitats. Distribution and habitat selection of animals is likely to vary by season (e.g. Ryan, Knechtel & Getz, 2006) and definitely does so in this NP (Caro, 1999*a*). For simplicity and because surveys were not carried out in the same years and seasons, we fitted separate models for dry and wet seasons. If animals used open habitat more often than expected based on availability, we termed this as 'preference' for open habitat. Given that most of our data samples were not repeated within short time periods, we were not able to estimate detection functions (e.g. MacKenzie *et al.*, 2003); hence, habitat 'preference' coefficients need to be interpreted cautiously because vegetation dependent variation in species detectability might have biased statistical inference.

For the aerial data, we fitted fixed-effects logistic regression models for each species, and tested the effect of habitat type and location of the grid (all four different definitions of periphery separately vs. core of the NP). We included the year of the survey to test for temporal trends. As for the vehicle transect data analyses, we fitted models for wet and dry seasons separately.

For ground and aerial presence data, we fitted a range of *a priori* defined candidate models (including an intercept-only model) and used an information theoretic approach to select the most parsimonious model (Burnham & Anderson, 2002). For the ground data, we used Akaike's information criteria (AIC) and AIC weights; for the aerial models, we used the sample size corrected AICc and corresponding weights (Burnham & Anderson, 2002). This approach allowed us to identify whether adding a term for defining periphery (the distance to the nearest park boundary as a linear predictor for the ground data or a two-level factor core vs. periphery for the aerial data) would improve the model's performance, and if so to identify which of the periphery definitions (5 or 10 km CPP or LEP) would explain animal presence best. Because support for candidate models was often very similar, we used model averaging to generate weighted effect sizes (Burnham & Anderson, 2002).

Results

Vehicle transect-based distribution models

For the dry season data, there was support that occupancy of elephants and possibly buffalo was affected by distance to the park boundary (Table 1). In both species, occupancy increased with distance to the park boundary, thus lending support to the CPP hypothesis. Additionally, occupancy of these species was higher in open habitat compared with woodland (Table 2). Occupancy of zebra, topi and warthog, and all wildlife combined, was best explained by habitat (Table 1), with all species having higher occupancy in open habitats compared with woodland habitats (Table 2). Effect sizes for habitat were particularly strong in zebra and topi (Table 2). In giraffe, waterbuck and impala, occupancy was not related to any of the tested variables.

For the wet season data, we found that occupancy of waterbuck and all wildlife combined was affected by distance to park boundary (Table 1). Occupancy of waterbuck increased with increasing distance from the park boundary (supporting the CPP hypothesis). Also, occupancy of all wildlife combined slightly increased with distance to park boundary (supporting the CPP hypothesis) (Table 2). In elephant, buffalo, zebra, topi, warthog and wildlife combined, occupancy was mainly affected by habitat (Table 1), with occupancy being consistently higher in open habitats compared with woodlands. As for the dry season models, occupancy of giraffe and impala was not associated with our candidate variables (Table 1).

Aerial survey-based distribution models

Distributional models based on aerial censuses conducted during dry seasons lend little support for either CPP or LEP hypotheses (Table 3). Nonetheless, we found support for the CPP hypothesis in giraffe (Table 3), which had lower occupancy in the outer 5-km band of the park compared with the core areas of the park (although this regression coefficient was associated with a large standard error). In addition to finding little model selection support for variables

Table 1 Support for generalized mixed-effects linear models with binomial error structure (transect ID was entered as random factor) explaining presence of eight species detected during ground vehicle transects in Katavi National Park, Tanzania in 1995 and 1996

		Elephant			Giraffe			Buffalo			Zebra			Topi			Waterbuck			Warthog			Impala			Wildlife		
Season	Model	AIC	Δ_i	w_i	AIC	Δ_i	w_i	AIC	Δ_i	w_i	AIC	Δ_i	w_i	AIC	Δ_i	w_i	AIC	Δ_i	w_i	AIC	Δ_i	w_i	AIC	Δ_i	w_i	AIC	Δ_i	w_i
Dry	Habitat + Edge	632.00	0.00	0.65	1018.00	3.00	0.09	1093.00	0.00	0.48	891.80	1.80	0.29	649.40	1.90	0.28	1117.00	3.00	0.09	1142.00	1.00	0.38	567.80	2.50	0.12	3361.00	1.00	0.38
	Edge	641.60	9.60	0.01	1016.00	1.00	0.25	1093.00	0.00	0.48	949.00	59.00	0.00	706.10	58.60	0.00	1115.00	1.00	0.25	1173.00	32.00	0.00	567.30	2.00	0.15	3414.00	54.00	0.00
	Habitat	633.30	1.30	0.34	1016.00	1.00	0.25	1098.00	5.00	0.04	890.00	0.00	0.71	647.50	0.00	0.72	1115.00	1.00	0.25	1141.00	0.00	0.62	565.80	0.50	0.32	3360.00	0.00	0.62
	Intercept	647.40	15.40	0.00	1015.00	0.00	0.41	1104.00	11.00	0.00	950.60	60.60	0.00	705.40	57.90	0.00	1114.00	0.00	0.41	1173.00	32.00	0.00	565.30	0.00	0.41	3421.00	61.00	0.00
Wet	Habitat + Edge	248.70	1.50	0.19	600.00	3.00	0.10	472.50	1.30	0.34	549.00	1.70	0.26	507.30	1.50	0.32	634.50	0.00	0.76	329.70	1.70	0.26	317.90	3.80	0.08	1959.00	0.00	0.50
	Edge	249.60	2.40	0.12	598.00	1.00	0.27	495.50	24.30	0.00	552.80	5.50	0.04	540.20	34.40	0.00	641.20	6.70	0.03	333.50	5.50	0.04	316.00	1.90	0.20	2003.00	44.00	0.00
	Habitat	247.20	0.00	0.40	599.00	2.00	0.17	471.20	0.00	0.66	547.30	0.00	0.60	505.80	0.00	0.68	637.00	2.50	0.21	328.00	0.00	0.60	316.00	1.90	0.20	1959.00	0.00	0.50
	Intercept	247.90	0.70	0.29	597.00	0.00	0.46	502.30	31.10	0.00	550.90	3.60	0.10	538.20	32.40	0.00	648.20	13.70	0.00	331.50	3.50	0.10	314.10	0.00	0.52	2006.00	47.00	0.00

The distance to the closest border of the national park ('Edge') entered as a linear predictor; 'Habitat' was classified as 'open habitat' or 'woodland'. Models were fitted for dry and wet seasons separately. AIC is Akaike's information criteria, Δ_i is the difference in AIC, and w_i is the AIC weight based on all models (Burnham & Anderson, 2002).

Table 2 Model averaged regression coefficients (β) and Standard errors (SE) for candidate variables associated with the presence of eight species detected during ground vehicle transects in Katavi National Park, Tanzania in 1995 and 1996

	Elephant		Giraffe		Buffalo		Zebra		Topi		Waterbuck		Warthog		Impala		Wildlife	
Season	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE
Dry																		
Intercept	−3.265	0.289	−2.122	0.184	−2.391	0.285	−2.972	0.315	−3.604	0.314	−2.263	0.434	−2.255	0.219	−3.356	0.558	−0.431	0.159
OH	0.545	0.144	−0.057	0.054	0.421	0.181	1.293	0.172	1.806	0.251	0.079	0.188	0.571	0.099	0.091	0.075	0.714	0.094
Edge	0.022	0.010	−0.008	0.009	0.022	0.008	0.005	0.009	0.002	0.012	0.010	0.019	−0.007	0.007	−0.001	0.013	0.005	0.006
REI	0.530		0.323		0.616		0.638		0.504		0.986		0.439		1.236		0.345	
Wet																		
Intercept	−4.270	0.469	−2.927	0.292	−4.183	0.393	−3.555	0.553	−3.831	0.365	−3.806	0.542	−3.885	0.301	−4.346	0.699	−1.526	0.248
OH	0.427	0.258	0.002	0.073	1.563	0.297	0.549	0.230	1.617	0.293	0.722	0.231	0.742	0.309	0.032	0.105	0.818	0.119
Edge	−0.014	0.021	−0.015	0.014	0.013	0.014	0.006	0.013	−0.011	0.014	0.058	0.027	−0.009	0.014	−0.007	0.017	0.009	0.009
REI	0.783		0.544		0.658		1.196		0.608		1.141		0.320		1.459		0.546	

'OH' is the habitat variable ('open habitat' compared with 'woodland'); 'Edge' is the linear distance to the nearest border of the park, and 'REI' denotes the standard deviation of the random-effects intercepts.

Table 3 Support for generalized fixed-effects linear models with binomial error structure explaining presence of seven species detected during systematic reconnaissance flights conducted in Katavi National Park, Tanzania from 1988 to 2009

		Elephant			Giraffe			Buffalo			Zebra			Topi			Waterbuck			Warthog		
Season	Model	AICc	Δ_i	w_i	AICc	Δ_i	w_i	AICc	Δ_i	w_i	AICc	Δ_i	w_i	AICc	Δ_i	w_i	AICc	Δ_i	w_i	AICc	Δ_i	w_i
Dry	Year × 10 km LEP + Habitat	138.64	3.82	0.04	136.82	4.96	0.02	193.41	3.59	0.03	197.02	3.10	0.05	158.10	3.57	0.05	83.63	1.73	0.06	131.58	5.63	0.01
	Year × 5 km LEP + Habitat	138.77	3.95	0.03	135.80	3.94	0.03	193.84	4.02	0.03	197.63	3.71	0.04	158.09	3.56	0.05	85.30	3.40	0.03	130.63	4.68	0.02
	Year × 10 km CPP + Habitat	136.66	1.84	0.09	136.55	4.69	0.02	192.15	2.33	0.06	197.01	3.09	0.05	157.94	3.41	0.05	84.08	2.19	0.05	130.51	4.56	0.02
	Year × 5 km CPP + Habitat	138.61	3.79	0.04	132.71	0.85	0.12	193.81	3.99	0.03	197.66	3.74	0.04	158.29	3.76	0.05	85.95	4.05	0.02	131.57	5.62	0.01
	Year × 10 km LEP	142.62	7.80	0.00	136.59	4.73	0.02	196.14	6.32	0.01	199.95	6.03	0.01	164.51	9.98	0.00	84.07	2.17	0.05	129.54	3.60	0.03
	Year × 5 km LEP	142.44	7.62	0.01	136.42	4.56	0.02	196.50	6.68	0.01	200.27	6.35	0.01	163.27	8.74	0.00	85.28	3.38	0.03	128.54	2.60	0.06
	Year × 10 km CPP	140.56	5.74	0.01	136.49	4.63	0.02	194.52	4.70	0.02	200.09	6.17	0.01	164.36	9.83	0.00	84.68	2.78	0.04	128.45	2.51	0.06
	Year × 5 km CPP	141.79	6.97	0.01	134.66	2.80	0.05	196.38	6.56	0.01	200.22	6.30	0.01	163.31	8.78	0.00	86.15	4.25	0.02	129.66	3.72	0.03
	Year + Habitat + 10 km LEP	136.61	1.79	0.10	134.99	3.13	0.04	191.78	1.96	0.08	195.60	1.68	0.10	156.50	1.97	0.11	83.48	1.58	0.07	130.51	4.57	0.02
	Year + Habitat + 5 km LEP	136.85	2.03	0.09	134.17	2.31	0.06	191.81	1.99	0.08	195.92	2.00	0.09	156.44	1.91	0.12	83.71	1.81	0.06	130.16	4.22	0.02
	Year + Habitat + 10 km CPP	136.62	1.80	0.10	135.03	3.17	0.04	190.13	0.31	0.18	195.10	1.18	0.13	156.50	1.97	0.11	83.88	1.98	0.06	130.43	4.49	0.02
	Year + Habitat + 5 km CPP	136.85	2.03	0.09	131.86	0.00	0.19	191.78	1.96	0.08	195.89	1.97	0.09	156.55	2.02	0.11	83.95	2.05	0.05	130.05	4.11	0.03
	Year + 10 km LEP	140.59	5.77	0.01	134.75	2.89	0.04	194.52	4.70	0.02	198.53	4.61	0.02	162.92	8.39	0.00	83.93	2.03	0.05	128.50	2.55	0.06
	Year + 5 km LEP	140.53	5.71	0.01	134.78	2.92	0.04	194.47	4.65	0.02	198.58	4.66	0.02	161.64	7.11	0.01	83.72	1.82	0.06	128.10	2.15	0.07
	Year + 10 km CPP	140.53	5.71	0.01	134.97	3.11	0.04	192.51	2.69	0.05	198.18	4.26	0.03	162.92	8.39	0.00	84.48	2.58	0.04	128.41	2.46	0.06
	Year + 5 km CPP	140.03	5.21	0.02	133.79	1.93	0.07	194.36	4.54	0.02	198.46	4.54	0.02	161.60	7.07	0.01	84.15	2.25	0.05	128.16	2.21	0.07
	Year + Habitat	134.82	0.00	0.24	133.30	1.44	0.09	189.82	0.00	0.21	193.92	0.00	0.23	154.53	0.00	0.30	81.90	0.00	0.15	128.48	2.53	0.06
	Year	138.94	4.13	0.03	133.14	1.28	0.10	192.62	2.81	0.05	196.74	2.82	0.06	160.90	6.38	0.01	82.46	0.56	0.11	126.48	0.53	0.15
	Intercept only	137.12	2.30	0.08	141.89	10.03	0.00	195.18	5.36	0.01	202.89	8.97	0.00	164.01	9.48	0.00	91.88	9.98	0.00	125.95	0.00	0.20
Wet	Year × 10 km LEP + Habitat	99.48	6.70	0.01	161.66	5.77	0.01	209.90	5.59	0.01	169.38	3.27	0.05	146.12	1.61	0.13	107.41	2.08	0.05	137.15	4.14	0.02
	Year × 5 km LEP + Habitat	99.74	6.96	0.01	161.30	5.41	0.01	208.83	4.52	0.02	166.11	0.00	0.27	150.06	5.55	0.02	109.04	3.71	0.02	135.48	2.47	0.05
	Year × 10 km CPP + Habitat	98.84	6.07	0.02	161.90	6.01	0.01	206.62	2.31	0.05	170.09	3.98	0.04	147.33	2.82	0.07	108.46	3.13	0.03	138.61	5.60	0.01
	Year × 5 km CPP + Habitat	100.10	7.32	0.01	161.89	6.00	0.01	209.50	5.19	0.01	170.29	4.18	0.03	149.41	4.90	0.02	109.96	4.63	0.01	139.28	6.27	0.01
	Year × 10 km LEP	97.40	4.63	0.03	159.71	3.82	0.03	208.09	3.78	0.03	183.00	16.89	0.00	150.15	5.64	0.02	106.34	1.01	0.08	136.02	3.01	0.04
	Year × 5 km LEP	97.74	4.96	0.03	159.55	3.66	0.03	207.38	3.07	0.04	177.23	11.12	0.00	153.31	8.80	0.00	108.39	3.06	0.03	133.86	0.85	0.11
	Year × 10 km CPP	96.77	3.99	0.04	159.98	4.09	0.03	204.81	0.50	0.13	183.30	17.19	0.00	151.32	6.81	0.01	107.16	1.83	0.06	137.48	4.47	0.02
	Year × 5 km CPP	98.12	5.34	0.02	159.98	4.09	0.03	207.77	3.46	0.03	180.65	14.54	0.00	152.48	7.97	0.01	109.12	3.79	0.02	137.89	4.88	0.01
	Year + Habitat + 10 km LEP	97.83	5.05	0.03	159.79	3.90	0.03	207.84	3.53	0.03	168.43	2.32	0.08	144.51	0.00	0.28	107.00	1.67	0.06	135.22	2.21	0.05
	Year + Habitat + 5 km LEP	97.67	4.90	0.03	159.24	3.35	0.04	206.77	2.46	0.05	168.17	2.06	0.10	148.14	3.63	0.05	107.48	2.15	0.05	135.57	2.56	0.05
	Year + Habitat + 10 km CPP	98.76	5.99	0.02	159.83	3.94	0.03	208.09	3.78	0.03	168.17	2.06	0.10	146.06	1.55	0.13	107.81	2.48	0.04	136.55	3.54	0.03
	Year + Habitat + 5 km CPP	98.08	5.30	0.02	159.83	3.94	0.03	208.04	3.73	0.03	168.25	2.14	0.09	148.10	3.59	0.05	108.11	2.78	0.03	137.21	4.20	0.02
	Year + 10 km LEP	95.77	3.00	0.07	157.85	1.97	0.08	206.04	1.74	0.07	181.98	15.88	0.00	148.57	4.07	0.04	105.92	0.60	0.10	134.10	1.09	0.10
	Year + 5 km LEP	95.69	2.91	0.08	157.50	1.62	0.09	205.32	1.02	0.10	179.47	13.37	0.00	151.36	6.86	0.01	106.85	1.53	0.06	133.97	0.96	0.10
	Year + 10 km CPP	96.70	3.93	0.05	157.91	2.03	0.07	206.28	1.98	0.06	181.38	15.28	0.00	150.07	5.57	0.02	106.51	1.19	0.08	135.44	2.43	0.05
	Year + 5 km CPP	96.11	3.34	0.06	157.93	2.05	0.07	206.32	2.02	0.06	178.65	12.55	0.00	151.25	6.75	0.01	107.29	1.97	0.05	135.84	2.83	0.04
	Year + Habitat	96.82	4.04	0.04	157.78	1.90	0.08	206.11	1.81	0.07	166.38	0.28	0.23	146.08	1.58	0.13	106.49	1.17	0.08	135.29	2.28	0.05
	Year	94.77	2.00	0.12	155.89	0.00	0.20	204.31	0.00	0.17	179.94	13.83	0.00	149.62	5.11	0.02	105.33	0.00	0.14	134.33	1.32	0.09
	Intercept only	92.78	0.00	0.32	156.73	0.84	0.13	213.53	9.22	0.00	182.92	16.81	0.00	161.32	16.81	0.00	110.61	5.28	0.01	133.01	0.00	0.16

We considered four different definitions of edge areas: a band of 5 and 10 km inside the borders of the national park was used to test the 'core–periphery phenomenon' (5 and 10 km CPP); to test the 'local exploitation-phenomenon', we defined grids within 5 and 10 km in the northern and southern border as edge areas (5 and 10 km LEP). Models were fitted for dry and wet season separately. 'Habitat' was classified as 'open habitat' or 'woodland'. AICc is the sample sized corrected Akaike's information criteria, Δ_i is the difference in AICc and w_i is the AICc weight based on all models (Burnham & Anderson, 2002).

associated with either CPP of LEP hypotheses, the model averaged coefficients for these variables showed inconsistent trends for the effect size across species (Table 4). In most species (elephant, buffalo, zebra, topi and waterbuck), the most supported models explaining occupancy contained year and habitat (Table 3). In all these species, dry season occupancy had declined over time and was higher in open habitat compared with woodland habitat (Table 4). Despite a decline over time in occupancy observed in many species, there was no support for the hypothesis that occupancy would decline faster in the periphery of the NP or in areas assumed to be subject to considerable human exploitation.

Wet season distribution models suggested that distribution of zebra (5 km LEP) and topi (10 km LEP) was possibly associated with the southern and northern borders of the park (Table 3). Zebra occupancy was higher in the core versus the 5-km band to the north and south (supporting the LEP hypothesis), whereas topi occupancy was lower in the core versus the 10-km band to the north and south. In zebra, we also found evidence for a time–edge interaction term, suggesting that zebra occupancy was slightly increasing in the 5-km periphery over time. In both species, however, regression coefficients of the LEP terms (and the year–LEP interaction in zebra) were associated with large margins of error (Table 4). Occupancy of giraffe, buffalo and waterbuck was best explained by year of the survey (Table 3); in all species, wet season occupancy had declined over time.

Discussion

We found little support for either CPP or LEP in this African NP despite our focus on large mammals that are sought after by illegal hunters entering the NP (Caro, 2008; Martin & Caro, in press). Results pertaining to CPP are especially robust because they were generated by two independent sampling methods: ground transects and aerial censuses. Specifically, we found that only elephant and perhaps buffalo were found more frequently in the core of the park rather than on its periphery as based on ground transects conducted during the dry season. We assume that the availability of surface water in the central parts of Katavi is an important factor for these species (Caro, 1999*a*). Therefore, the majority of herbivore species that we examined do not appear to 'avoid' the park periphery even in the dry season. Moreover, five species (giraffe, buffalo, zebra, topi and waterbuck) have declined over time, as based on occupancy data examined here, and several other species have declined as based on population sizes (examined elsewhere, Caro, 2011), yet there seems little evidence that declines occur mainly in edge areas of the NP. Surprisingly, given the extent of illegal hunting in this park, there was no evidence for LEP as based on aerial census data considering either a 5-km strip or a 10-km strip inside the park boundaries. At first sight, therefore, hunting pressure from illegal hunters does not seem to affect large mammal distributions to any detectable extent in this NP.

Before accepting these findings, however, we need to consider a number of methodological issues. The first potential concern is that our analyses were insufficiently fine-grained to detect strong spatial differences. We defined our edge categories derived from the aerial census data as distances of 5 or 10 km from the NP boundary, but it possible that edge effects are only manifested a very short distance from the boundary. This seems unlikely given that people are occasionally seen at some distances inside the NP (T. C., pers. obs.), that gunshots are heard in proximity to a tourist camp that is 8 km from the boundary, and that findings from a foot survey carried out in Katavi NP in 2004 suggest that most illegal activities occur within *c.* 5–10 km of the NP border (see Fig 1 in Waltert, Meyer & Kiffner, 2009). Moreover, other studies in Africa estimate highest poaching probabilities within 5 km of protected area borders, that of Lindsey *et al.* (2011) in Savé Valley Conservancy, Zimbabwe, for example.

Second, mammals may be easier to see in open habitats (e.g. MacKenzie *et al.*, 2003; Gu & Swihart, 2004), and edge areas and habitat types were confounded to some degree. The vehicle transects traversed mainly woodland near the park boundaries and mainly open habitat in the core areas of the park; a logistic regression showed a significant relationship between distance to park boundary and likelihood of traversing open habitat. For the aerial design, we only found significant confounding between habitat and edge definitions for the 5-km CPP hypothesis. These findings suggest that detectability might have been lower in the periphery (more woodland) versus core of the park (more open vegetation). Nonetheless, we focused on species that can be detected reasonably well from the air (Jachman, 2002), and the findings from our analyses (absence of edge effects) suggest that occupancy in the core versus periphery was not substantially biased.

The third methodological concern is that we did not record relevant variables that might have overridden edge effects, such as food (Ryan *et al.*, 2006) and surface water availability (Redfern *et al.*, 2003; Ryan *et al.*, 2006; Ogutu *et al.*, 2010), or predation risk by natural predators (Valeix *et al.*, 2011). Nonetheless, these factors were – at least partially – accounted for by the random-effects model used for the ground data. Fourth, the small sample size of presences recorded for some species during aerial surveys might have further impeded detecting a significant signal of the spatial contrasts. Finally, for the aerial occupancy models, we did not consider factors that account for spatial and temporal autocorrelation of occupancy of the grid cells. Albeit occupancy of a grid cell by a given species is likely to be affected by occupancy of the same species in neighbouring cells, and whether the cell was occupied in a previous survey, failure to account for these potential dependencies is unlikely to affect our main conclusion; effect sizes might overestimate 'true' effect sizes, but it is unlikely that edge hypotheses would be supported if we had included autocorrelation terms.

Despite these methodological concerns, effects of CPP and LEP might be absent, weak or undetectable given available data for all species in this NP. This is partially supported by data collected in the same NP using systematically

Table 4 Model averaged regression coefficients (β) and standard errors (SE) for candidate variables associated with the presence of seven species detected during systematic reconnaissance flights conducted in Katavi National Park, Tanzania from 1988 to 2009

	Elephant		Giraffe		Buffalo		Zebra		Topi		Waterbuck		Warthog	
Season	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE
Dry														
Intercept	32.162	79.813	254.792	93.882	132.923	67.045	163.087	62.822	165.495	75.812	1174.030	56391.191	–116.273	105.414
Year	–0.632	23.578	–13.623	9.779	–7.709	11.501	–28.474	11.676	–47.062	34.485	–10 128.510	177 620 189.607	–86.939	31.546
OH	1.077	1.805	0.569	0.406	0.691	0.373	0.672	0.382	1.076	0.508	–1.759	211.831	–0.039	0.215
5 km CPP	–4.076	6.587	–29.882	29.048	–0.360	4.893	2.907	5.780	4.552	8.502	–3.247	13.801	–8.029	10.711
10 km CPP	–8.514	17.834	–5.025	7.485	1.405	11.030	2.885	8.052	6.844	8.904	43.719	33.536	–27.175	19.811
5 km LEP	0.421	1.238	1.980	3.329	0.086	1.286	–0.901	1.661	–0.572	1.130	–102.779	9959.888	19.048	15.487
10 km LEP	0.170	6.798	2.487	5.521	–3.663	5.851	–5.643	7.243	–5.208	7.923	–486.179	46 278.820	10.344	10.396
Year × 5 km CPP	0.002	0.004	0.015	0.015	0.000	0.002	–0.001	0.003	–0.002	0.004	0.002	0.007	0.004	0.005
Year × 10 km CPP	0.004	0.009	0.003	0.004	–0.001	0.005	–0.001	0.004	–0.003	0.004	–0.022	0.017	0.014	0.010
Year × 5 km LEP	0.000	0.001	–0.001	0.002	0.000	0.001	0.000	0.001	0.000	0.001	0.052	5.002	–0.010	0.008
Year × 10 km LEP	0.000	0.003	–0.001	0.003	0.002	0.003	0.003	0.004	0.003	0.004	0.244	23.243	–0.005	0.005
Wet														
Intercept	13.150	97.975	115.636	81.129	278.551	97.546	1414.983	104 026.046	338.850	119.954	314.027	145.311	809.661	70 089.684
Year	–0.008	0.049	–0.059	0.041	–0.141	0.049	–0.713	52.325	–0.171	0.060	–0.159	0.073	–0.408	35.256
OH	–0.023	0.145	0.072	0.171	0.080	0.136	1.669	0.436	1.071	0.427	0.254	0.240	0.141	0.154
5 km CPP	–2.046	7.954	1.405	10.128	–4.942	6.352	1.245	6.233	5.842	6.946	4.239	8.854	–1.372	6.081
10 km CPP	4.312	14.362	0.522	6.610	–62.699	36.332	2.349	6.159	–19.439	24.061	25.172	21.922	1.710	7.524
5 km LEP	2.024	14.729	–0.929	6.975	0.909	9.058	–1242.973	103 962.176	2.014	5.173	–11.195	16.430	–719.485	69 989.829
10 km LEP	–7.317	11.514	3.602	7.876	0.688	5.326	–9.306	8.918	19.821	30.153	–42.900	34.445	–7.180	17.324
Year × 5 km CPP	0.001	0.004	–0.001	0.005	0.002	0.003	–0.001	0.003	–0.003	0.003	–0.002	0.004	0.001	0.003
Year × 10 km CPP	–0.002	0.007	0.000	0.003	0.031	0.018	–0.001	0.003	0.010	0.012	–0.013	0.011	–0.001	0.004
Year × 5 km LEP	–0.001	0.007	0.000	0.003	–0.001	0.005	0.625	52.292	–0.001	0.003	0.006	0.008	0.362	35.206
Year × 10 km LEP	0.004	0.006	–0.002	0.004	0.000	0.003	0.005	0.004	–0.010	0.015	0.021	0.017	0.004	0.009

‘OH’ is the habitat variable ‘open habitat’ (compared with ‘woodland’). We considered four different definitions of edge areas and compared the likelihood of animal presence in these edge areas with those in the core of the national park: a band of 5 and 10 km inside the borders of the national park was used to test the ‘core–periphery phenomenon’ (5 and 10 km CPP compared with core areas); to test the ‘local exploitation phenomenon’, we defined grids within 5 and 10 km in the northern and southern border as edge areas (core areas compared with 5 and 10 km LEP).

distributed foot surveys during the dry season 2004 (Kiffner *et al.*, 2009). This study, like ours, found a lack of effect of location at the species level (except for topi), although, in contrast to our findings which uncovered no effect of location on combined wildlife occupancy, this earlier study did find a significant correlation between distance to the NP boundary and abundance of 16 species of herbivores combined.

Parallel support for an absence of effects of CPP and LEP comes from a recent, similar study conducted in the Masai Mara National Reserve, Kenya. There, Ogutu *et al.* (2011) conducted similar analyses (defining a 5-km edge area within the protected area) based on aerial surveys conducted from 1977 to 2009, and found that species' declines over time occurred uniformly throughout the protected area.

What could be responsible for the absence of LEP effects in Katavi NP and potentially other protected areas? There is no doubt that illegal hunting occurs in Katavi NP, and it has been conjectured that hunting may be responsible for the numerous declines in large mammal populations there (Caro, 2008), although, more recently, changing water flows within the NP may also be involved (Manase, Gara & Wolanski, 2011). One possibility is that hunters prefer to hunt in certain habitats or locations, which could override any edge effects. Certainly, data from interviews with illegal hunters indicate that they prefer to hide in thick bush to avoid detection by anti-poaching patrols (Martin *et al.*, unpubl. data). Another possibility is that herbivore birth rates are sufficiently high in the park centre that individuals disperse from their natal area, and thereby re-establish or refill their populations in areas that have been heavily hunted. If animals do not take account of predation risk by humans, they might redistribute themselves according to an ideal free distribution (Fretwell & Lucas, 1970) and succumb to an 'ecological hunting trap' (Schlaepfer, Runge & Sherman, 2002). In short, local sink-source dynamics might occur, but we might be unable to detect them if they are compensated by movements and re-distribution. Thus, a more sensible approach for determining habitat suitability would be to assess the spatial distribution of population growth or decline in target species (e.g. Mosser *et al.*, 2009).

It is worth noting that our species-specific results for large herbivores contrast those found for lions *Panthera leo* in the same NP; lions were less likely to occur within 3 km of the edge of the NP than in the centre of the NP (Kiffner *et al.*, 2009). Besides being targeted by trophy hunters outside the park, which could create a 'vacuum-effect' (Loveridge *et al.*, 2007), lions are also hunted by Sukuma (a pastoralist ethnic group) young men on foot inside the NP (Borgerhoff Mulder *et al.*, 2009), both of which may be responsible for reduced lion densities inside NP borders. It is interesting that in carnivores that have larger home ranges for a given body weight than herbivores (Carbone & Gittleman, 2002), edge effects are manifested in spatial distribution of the population, whereas this seems not to be the case for large herbivores.

This is the fourth publication to demonstrate that wildlife populations are in broad decline in this ecosystem (see also Stoner *et al.*, 2007*b*; Caro, 2008; Caro, 2011). Analyses here indicate that buffalo, giraffe, topi, waterbuck and zebra populations have all seen declines within the confines of the old NP itself. Based on aerial surveys, significant declines in population sizes have been reported for six additional herbivore species as well (Stoner *et al.*, 2007*b*). Ground censuses have additionally shown that lion and spotted hyaena *Crocuta crocuta* populations are declining (Caro, 2011). Reductions in this many species should be a cause for serious concern. Changing water levels due to water diversion outside the NP, widespread illegal hunting or both are likely to be responsible (Caro *et al.*, unpubl. data). Patterns of wildlife decline in this area suggest that both issues need urgent attention.

In conclusion, this analysis of large herbivore distributions did not find substantial differences in large mammal species distributions between the park periphery and core despite widespread declines in occupancy and population sizes over time. These findings suggest that we cannot necessarily assume that all exploited species will be subject to edge effects (CPP) in a manner that conservation theory would suggest. Furthermore, our analysis of large herbivore distributions relatively near to human settlements in an area known for illegal hunting (LEP) did not uncover reduced herbivore occupancy inside the park periphery. At present, we cannot distinguish whether population declines over time are caused by processes primarily occurring from reserve boundaries inwards as theory would suggest, or whether these declines are caused by processes occurring more homogenously in space. However, processes that cause these declines in wildlife species apparently do not manifest themselves in predicted changes in spatial distribution patterns.

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