BIODIVERSITY RESEARCH

An empirical evaluation of the African elephant as a focal species for connectivity planning in East Africa

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ABSTRACT

Aim Large, charismatic and wide-ranging animals are often employed as focal species for prioritizing landscape linkages in threatened ecosystems (i.e. 'connectivity conservation'), but there have been few efforts to assess empirically whether focal species co-occur with other species of conservation interest within potential linkages. We evaluated whether the African elephant (*Loxodonta africana*), a world-recognized flagship species, would serve as an appropriate focal species for other large mammals in a potential linkage between two major protected area complexes.

Location A 15,400 km² area between the Ruaha and Selous ecosystems in central Tanzania, East Africa.

Methods We used walking transects to assess habitat, human activity and co-occurrence of elephants and 48 other large mammal species (> 1 kg) at 63 sites using animal sign and direct sightings. We repeated a subset of transects to estimate species detectability using occupancy modelling. We used logistic regression and AIC model selection to characterize patterns of elephant occurrence and assessed correlation of elephant presence with richness of large mammals and subgroups. We considered other possible focal species, compared habitat-based linear regression models of large mammal richness and used circuit theory to examine potential connectivity spatially.

Results Elephants were detected in many locations across the potential linkage. Elephant presence was highly positively correlated with the richness of large mammals, as well as ungulates, carnivores, large carnivores and species > 45 kg in body mass ('megafauna'). Outside of protected areas, both mammal richness and elephant presence were negatively correlated with human population density and distance from water. Only one other potential focal species was more strongly correlated with species richness than elephants, but detectability was highest for elephants.

Main conclusions Although African elephants have dispersal abilities that exceed most other terrestrial mammals, conserving elephant movement corridors may effectively preserve habitat and potential landscape linkages for other large mammal species among Tanzanian reserves.

Keywords
African elephant, connectivity, corridor, focal species, large mammals, protected area.

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INTRODUCTION

The focal species concept and related variations (e.g. umbrella, surrogate indicator or landscape species) strive to address the conservation or management needs of whole communities by focusing on the requirements of a species subset (Lambeck, 1997). Although widely debated (Simberloff, 1998; Caro & O'Doherty, 1999; Lindenmayer & Fischer, 2003; Wiens *et al.*,

2008), the focal species concept is now a staple of landscape planning for wildlife management and conservation because it allows action with incomplete knowledge. Increasingly, the approach is used not only to design protected areas (e.g. Noss *et al.*, 1999) but also to plan wildlife linkages (i.e. corridor networks for multiple species) to maintain connectivity among protected areas (e.g. Sanderson *et al.*, 2002b; Rouget *et al.*, 2006; Thorne *et al.*, 2006; Beier *et al.*, 2008). While many studies have analysed spatial overlap among focal and non-focal species in core protected areas, the efficacy of the focal species approach for planning habitat connectivity outside of protected areas has seldom been tested.

Wildlife linkages are proposed to facilitate two processes: (1) direct movement among core habitat areas by 'passage species' and (2) connectivity and gene flow through local interactions for dispersal-limited 'corridor dwellers' that rely on persistence within the linkage (Beier *et al.*, 2008). Both processes are species specific and scale dependent. Most linkage designs rely heavily on focal species (Beier *et al.*, 2008), under the assumption that habitat linkages modelled on the needs of a single species or small suite of species serve many other species through both processes. Furthermore, many of these designs assume that species known to be good focal species in core areas will have a similar role in less-protected habitats. However, for many species, both dispersal and the distribution of species outside core areas are poorly understood (Hilty *et al.*, 2006). Thus, the choice of appropriate surrogates for linkage planning typically relies on expert opinion and literature review (Beier *et al.*, 2008).

Here, we conducted an empirical assessment of the distribution of large mammals across an expansive and heterogeneous landscape in East Africa to examine how the focal species approach could inform linkage planning in this ecosystem. The large mammal communities of East Africa exemplify the challenges for connectivity conservation because they are highly diverse and include many species prone to conflict with or exploitation by humans, such as African elephant (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*), African buffalo (*Syncerus caffer*), large carnivores and dozens of ungulate species (Newmark, 2008). Numerous protected areas in this region were established in the 19th and 20th centuries, often with the aim of preserving dry-season refuges for plains game and other species. However, many species have declined (Stoner *et al.*, 2007) or disappeared from reserves (Newmark, 1996), and it is argued widely that maintaining or creating habitat connectivity among protected areas is critical to the persistence of large mammals in East Africa (Soule *et al.*, 1979; Newmark, 2008). Nearly all East African protected areas are unfenced, allowing animal movements in and out of reserves and enabling some critical seasonal migrations (Bolger *et al.*, 2008). While many species of large mammals may persist outside of protected areas in East Africa, differences in habitat needs, sensitivity to human disturbances and local threats greatly complicate strategies for conserving connectivity between reserves (Caro *et al.*, 2009).

We evaluated patterns of co-occurrence of large (> 1 kg) mammal species (nomenclature as in Kingdon, 1997) and guilds in a potential linkage in central Tanzania that links two of the largest reserve complexes in the world, the Ruaha and Selous ecosystems. Specifically, we sought to determine the degree to which the landscape (connectivity) needs of one focal species, the African elephant, also encompass habitats utilized by other mammals in its community. African elephants (hereafter 'elephants') have been used as focal species in connectivity design (e.g. Rouget *et al.*, 2006; Plumptre *et al.*, 2007) because of their large area requirements (Estes, 1991) and because they are (1) easily observed (e.g. from the air, by local people, or by searching for tracks or dung), (2) highly sensitive to human activity (Hoare, 2000) and (3) considered a conservation flagship species with high value for tourism and regulated trophy hunting. On the other hand, elephants may be poor surrogates for other large mammals because they thrive in a wide variety of habitats, their diet is highly variable, they are behaviourally complex and can cover great distances in a day without food or water (Estes, 1991).

Our study takes place in a region of Tanzania that is the focus of a current effort to identify and implement wildlife linkages (Jones *et al.*, 2009).The primary goals of our study were to (1) determine whether elephants and other large mammals occurred across a potential wildlife linkage among protected areas in central Tanzania, (2) identify habitat and other landscape features that best predicted the distribution of elephants or other species of large mammals within that linkage and (3) assess the value of elephants and other potential focal species in this ecosystem for planning and conserving landscape linkages.

METHODS

Assessing elephant activity and patterns of species occurrence

We surveyed both protected and unprotected habitat in central Tanzania in an area bounded by Ruaha National Park to the west (part of a large complex of park and game reserves), Mikumi National Park to the east (directly linked to the Selous Game Reserve) and Udzungwa Mountains National Park to the south (Fig. 1). We chose this region because it is the only remaining potential link between populations of large mammals in the Ruaha and Selous ecosystems. Moreover, initial investigations in the study area reported movements of elephant and other species outside reserves (B. Mbano, Wildlife Conservation Society, personal communication). The study area included fully protected areas (the national parks listed above), partially protected areas open to limited hunting or other extractive uses [e.g. Idodi-Pawaga Wildlife Management Area (WMA) and forest reserves including Image, West Kilombero Scarp (now Kilombero Nature Reserve), Pala Mountain, Mang'alisa and Ukwiva] and village lands and Game Controlled Areas (GCAs) of Iringa, Dodoma and Morogoro regions where agriculture, extractive use of

Figure 1 Transect locations (filled circles; scaled by number of large mammal species detected) and elephant presence/absence (cross) for 63 walking transects in central Tanzania (inset), with topographic relief (shading), lakes and rivers, and patrolled protected areas. Game Reserves (GR) and National Parks (NP) are delineated with thick lines; the Idodi-Pawaga Wildlife Management Area (WMA) is delineated with a dot-dashed line.
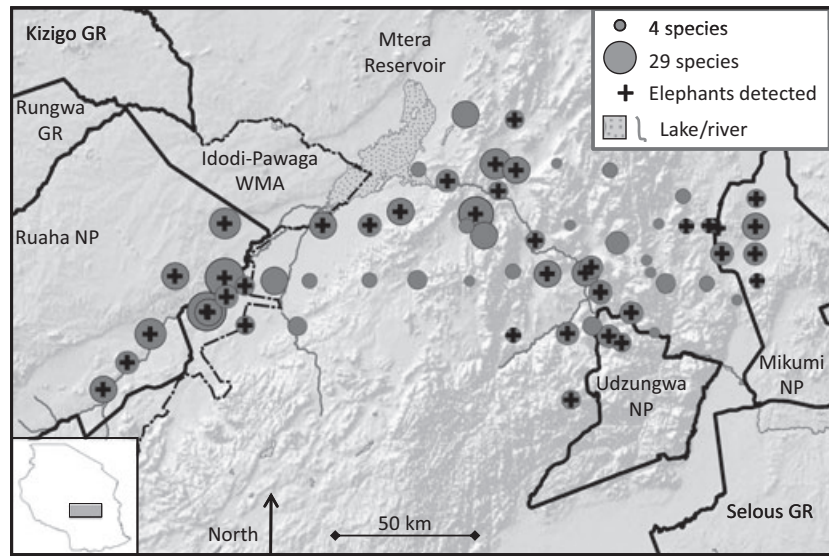
wildlife and forest resources, and human settlement (village lands) were either permitted or not typically deterred by enforcement. Hereafter, we use 'protected areas' to describe locations reported to have regular or semi-regular patrols, including parks, WMAs and transects in Kilombero Nature Reserve and Pala Mountain Forest Reserve, but not GCAs, which typically lack antipoaching enforcement and marked boundaries.

Our study area in central Tanzania displays a variable semi-arid climate with approximately 6 months of dry season followed by rain from November to April. Annual rainfall in the region is 380–650 mm with an average around 500 mm; elevations in the study area range from 350 to 2470 m. Vegetation in the region primarily includes species typical of acacia savanna, but transitions gradually to *miombo* (woodland savanna) towards the south. Higher elevation areas are characterized by montane woodland or montane forest.

We employed walking survey transects to assess presence/absence of elephants and other large (> 1 kg) mammals over a *c.* 15,400 km^2 area defined by mapping suspected elephant movement corridors based on interviews with wildlife officers (B. Mbano, personal communication) and extending the sampling area out by at least *c.* 30 km to buffer this area. We conducted 44 transects across the study area from September to early December 2006 and February 2007, and completed an additional 36 transects from August to November 2007 (Fig. 1). To assess species detectability, 17 transects surveyed in season 1 were resurveyed in season 2, yielding a total of 63 unique transect locations over the two seasons. Total length of transects surveyed on foot was 375 km in the first season, 298 km in the second season, and 673 km total. Length of walking transects (see Appendix S1 in Supporting Information) averaged 8.0 km (range 1.5–15 km, SD 2.9 km; Appendix S1).

Although many landscape-scale surveys of wildlife (particularly in East Africa) have been accomplished using vehicles, roads or existing foot trails (e.g. Traill & Bagalke, 2006), such study designs may under-represent some habitats or over-represent human activity. To reduce such bias, 50 of the 63 unique walking transect locations, triangular in shape to maximize the time spent surveying (Waltert *et al.*, 2008), were placed according to a randomly determined regular grid of points. We used a grid with 10-min (*c.* 19 km) spacing between points in most areas, although 5- and 7-min grids were initially employed in some of the protected areas (Appendix S1). The remaining 15 locations were surveyed using 'recce' style transects (Walsh & White, 1999), mostly off-trail, in areas where local people reported elephant activity.

During each transect, we recorded dung and tracks of all large (> 1 kg) mammals within *c.* 2.5 m of the transect centre line as well as large mammal sightings (Appendix S1). Sign identifications were discussed and recorded as 'confident' or 'not confident'; all analyses in this study are based solely on 'confident' sign identifications. In some cases, species with very similar tracks were combined into categories and treated as a single multi-species group in further analyses (Appendix S2). We scored tracking conditions (i.e. quality of the substrate for revealing prints) for each transect. We also recorded livestock grazing (sign or animals), farm fields under recent cultivation (not overgrown) and protected area status. Local people who accompanied our team were questioned about elephant activity and other mammal species in each area. Finally, we used a GIS to determine the elevation of a centrally located point for each transect, distance to major water sources (permanent rivers and lakes), distance to nearest protected area (Park, Game Reserve and WMA), human population density (ward level, from the 2002 Tanzania Census) and 'human influence' (Sanderson *et al.*, 2002a).

Testing the umbrella value of elephants

We evaluated the potential for direct movement or gene flow of elephants by mapping and visually assessing whether elephants were detected continuously across the study area.

We used Spearman rank tests to assess (1) whether elephant presence/absence was correlated ($P < 0.05$) with predictor variables describing human activity, human population density, protected area status and habitat as determined on transects and from remotely sensed data (Table 1) and (2) whether predictor variables used in our analyses were highly correlated ($r_s > 0.7$). To account for spatial autocorrelation, we used SAM (Rangel *et al.*, 2006) to calculate Dutilleul's (1993) modification of the significance test for the Pearson correlation coefficient.

We used logistic regression to model elephant presence/absence as a function of all predictor variables that were correlated with elephant detection at $P < 0.05$; if two predictor variables were correlated at $r_s > 0.7$, we retained only the most strongly correlated variable. We also included distance to water because it is often a key habitat variable for African elephants (e.g. Cushman *et al.*, 2010). We used the small-sample correction for Akaike's information criterion (AIC$_c$, Burnham & Anderson, 1998) to compare the global model (all variables) and a priori models with reduced numbers of predictor variables. After identifying predictor variables in competitive models (within 2 ΔAIC$_c$ values of the top-ranked model), we calculated AIC$_c$ weights for all possible combinations of models incorporating those variables. We ranked relative importance of each variable by summing the AIC$_c$ weights for all models containing that variable (Burnham & Anderson, 1998). Because spatial autocorrelation may increase the risk of Type I statistical errors (Sokal *et al.*, 1998), we used Moran's I to test for spatial autocorrelation in the residuals of the best model from each logistic regression analysis. We used distance classes of 5 km and tested for spatial autocorrelation out to 75 km. We applied a Bonferroni correction to significance tests for values of Moran's I in each distance class to determine whether an autoregressive term needed to be included in the logistic regression analyses (Betts *et al.*, 2006).

Next, we tested whether elephant occurrence was a reliable predictor of large mammal richness across the entire study area. We used Spearman rank correlation tests as well as Pearson correlation tests modified to account for spatial autocorrelation (Dutilleul, 1993) to assess the correlation of elephant detection with the number (or average number for repeated transects) of species detected at each transect. We also assessed the correlation of elephant detection with the species richness of subgroups including ungulates (non-marine Cetartiodactyla and Perissodactyla), carnivores, large carnivores (lion *Panthera leo*, spotted hyaena *Crocuta crocuta*, leopard *Panthera pardus*, wild dog *Lycaon pictus* and cheetah *Acinonyx jubatus*), megafauna (> 45 kg) and species recognized widely in this region and elsewhere as tolerant of some human activities (Kingdon, 1997; IUCN 2009). This last group includes the African civet (*Civettictis civetta*), genet sp. (see Appendix S2), hare sp., yellow baboon (*Papio cynocephalus*), mongoose sp. and vervet monkey (*Cercopithecus pygerythrus*). Finally, to evaluate elephants as focal species outside patrolled protected areas, we estimated the correlation of elephant occurrence with the above groups on the 40 transects in village lands and GCAs.

Evaluating other focal species and modelling large mammal richness

Besides elephants, species such as lion, leopard, hippo (*Hippopotamus amphibius*) and African buffalo have been proposed as focal or landscape species on other East African landscapes (Plumptre *et al.*, 2007). We evaluated whether other potential focal species (15 species of larger carnivores and ungulates thought to occur across the whole study area and detected more than once outside protected areas in our study; Appendix S2) could serve as surrogate species for linkage conservation. We determined Spearman rank correlation of

Variable	Source	Spearman r_s	P	Corrected d.f.*	Corrected P*
Protected area†‡	Transect	0.51	< 0.0001	43	< 0.001
Human population density	GIS (2002 census)	−0.41	0.001	53	< 0.001
Distance from protected area†	GIS	−0.41	0.001	52	0.013
Farm Field	Transect	−0.41	0.001	62	< 0.001
Transect length	Transect	0.32	0.011	51	0.053
Grazed	Transect	−0.27	0.030	61	0.03
Elevation	GIS	−0.27	0.033	46	0.027
Distance from water	GIS	−0.19	0.127	–	–
Average tracking conditions	Transect	0.12	0.333	–	–

Table 1 Spearman rank tests for correlation of elephant presence with habitat variables and human activity at 63 mammal survey transects in central Tanzania. Corrected degrees of freedom (d.f.) and *P* values account for reduced statistical power resulting from spatial autocorrelation (Dutilleul, 1993).

*We report corrected d.f. and *P* values only for variables with significant ($P < 0.05$) estimates of r_s.

†Variables correlated with each other at $r_s > 0.7$.

‡'Protected area' includes National Parks, Wildlife Management Areas, Pala Mountain Forest Reserves and Kilombero Nature Reserve.

each species' detections with large mammal richness in the 40 transects outside of protected areas.

We used multiple linear regression to model richness of large mammal species detected outside of protected areas using the same habitat variables and model selection and ranking techniques as we employed to model elephant presence/absence (Table 1). We log-transformed transect length and included an index of tracking conditions to correct for potential bias against detecting smaller taxa when tracking conditions were poor.

Accounting for unequal detectability

Estimates of species occurrence or richness may be biased by variation in detection probability (Dorazio et al., 2006). We estimated species-specific detection probabilities and repeated analyses of species richness (correlation with elephant presence and multiple regression based on transect characteristics) using species subsets that included only highly detectable species with single-visit detection probabilities (P_{det}) > 0.7 and > 0.9, respectively (Table S1). We used PRESENCE (Hines, 2006) to estimate detection probabilities for all species with at least two detections per visit for the subset of transects we sampled twice ($n = 17$). Because of this small sample size, we used model selection via AIC_c estimates to determine only whether protected area status or transect length affected probabilities of detection or occupancy and then estimated point or average detection probabilities under the best model. We also estimated the Pearson pairwise correlation coefficient for the number of all mammal species, ungulates and carnivores detected on the 17 repeated transects as a general test of the consistency of our transect survey methods.

Visualizing potential connectivity across the study area

To compare the potential for movement or gene flow across the study area, we used circuit-theoretic modelling of connectivity (McRae et al., 2008) on the basis of the continuity and distribution of species detections (rather than on resistance surfaces based on habitat). In doing so, we assumed that (1) species detections at any point within the linkage implied higher potential for movement and gene flow through that area and (2) detections over a greater portion of the linkage implied greater connectivity. Circuit theory is used to model ecological connectivity similar to electrical connectivity under the principle that, unlike in least-cost path modelling, connectivity increases with multiple pathways (McRae et al., 2008). For our circuit model, we chose species that had high (> 0.65) probability of detection and occurred either in all three reserves or in Mikumi and Ruaha National Parks (i.e. their range included most of the study area). We created a 1-km raster across the study area for each species based on the minimum distance to nearest detection on all transects. We used that raster as a resistance surface in CIRCUITSCAPE to model 'current' among three nodes (Ruaha, Mikumi and Udzungwa Mountains National Parks) or two nodes (Ruaha and Mikumi) for species not known to occur in Udzungwa Mountains (Rovero & De Luca, 2007). We mapped current density for nine species to assess visually the correspondence of areas with higher probabilities of passage by random-walk movements between those reserves.

RESULTS

Assessing elephant activity and patterns of species occurrence

Elephants were detected on adjacent transects across much of the hypothesized linkage, including 18 of 40 transects outside protected areas and 22 of 23 transects within protected areas (Fig. 1). On the 17 resurveyed transects, elephants were present at exactly the same transects (12/17) after 1 year, although in some locations the amount of sign varied widely between years. The number of large mammal species detected varied from 7 to 29 where elephants were present (39 transects) and from 4 to 18 where elephants were absent (24 transects; Fig. 1; Appendix S2).

Testing the umbrella value of elephants

At the transect level, elephant presence was strongly correlated with patrolled protected areas (as defined earlier) and negatively correlated with human population density, farming, grazing and elevation (Table 1). Transect length was not correlated with elephant presence at $P < 0.05$ after correcting for spatial autocorrelation (Table 1). The best multiple logistic regression models of elephant presence/absence (all transects) included human population density, protected area status, elevation, distance to water and transect length as predictor variables (Table 2). Sums of AIC_c weights (Σw_i) for each variable across all possible subsets of models including those variables were 1.0 (protected area), 0.98 (human population density), 0.55 (transect elevation), 0.54 (distance to water) and 0.47 (transect length), indicating that human population density and protected area status had much more explanatory power. For the 40 transects outside of patrolled protected areas, best models of elephant presence included combinations of elevation ($\Sigma w_i = 0.75$), human population density ($\Sigma w_i = 0.60$) and distance from water ($\Sigma w_i = 0.62$). Residuals for the best models in both analyses exhibited no significant spatial autocorrelation.

For all transects, and for the subset of 40 transects conducted outside of protected areas, the presence of elephants was strongly correlated with the richness of mammal species, ungulates, carnivores, large carnivores, mammals > 45 kg and mammals with detection probability > 0.7 and > 0.9, but not 'human-tolerant' species (Table 3). Species richness was higher where elephants occurred than where they were absent (mean ± SE = 15.5 ± 0.7, 9.8 ± 0.9, respectively; $t = 5.1$, $P < 0.0001$).

Table 2 Logistic regression models of elephant presence/absence with model selection by Akaike's information criterion (AIC_c); only the global model and models with $\Delta AIC_c < 2$ from the best model are reported.

Transect location and number (*n*)	Model	R^2	Area under ROC	*P*	ΔAIC_c	AIC_c weight
All transects (*n* = 63)	Human population density, transect length, protected area, elevation	0.45	0.90	< 0.0001	0	0.27
	Human population density, protected area*, elevation	0.42	0.86	< 0.0001	0.2	0.25
	Human population density, distance to water, transect length, protected area, elevation	0.47	0.91	< 0.0001	0.8	0.19
	Human population density, transect length, protected area	0.41	0.86	< 0.0001	1.3	0.14
	Human population density, protected area	0.38	0.83	< 0.0001	1.4	0.14
	Global (human population density, farm fields, distance to water, transect length, protected area, grazed, elevation)	0.48	0.90	<0.0001	5.8	0.01
Village lands and Game Controlled Areas (*n* = 40)	Human population density, distance to water, elevation	0.26	0.83	0.002	0.00	0.22
	Distance to water, elevation	0.21	0.80	0.003	0.2	0.19
	Human population density, elevation	0.21	0.76	0.003	0.3	0.18
	Human population density, distance to water	0.20	0.78	0.004	0.6	0.16
	Elevation	0.16	0.76	0.003	0.6	0.16
	Global (human population density, distance to water, elevation, grazing, distance to protected area, transect length, farming)	0.29	0.85	0.051	10.6	< 0.01

*'Protected areas' include National Parks, Wildlife Management Areas, Pala Mountain Forest Reserve and Kilombero Nature Reserve.

Modelling large mammal richness and evaluating other focal species

Here, of our candidate focal or landscape species (Appendix S2), only hyaenas were correlated more strongly than elephants (Table 3) with large mammal richness outside protected areas (Spearman rank test, $r_s = 0.74$, $P < 0.0001$) or including ($r_s = 0.68$, $P < 0.0001$) protected areas. Leopard detections were correlated with species number (all transects, Spearman $r_s = 0.36$, $P = 0.004$; outside protected areas, $r_s = 0.53$, $P = 0.0004$) but less strongly than elephants. No ungulate was more strongly correlated with species richness than elephants.

Outside of protected areas, the number of species detected per transect was negatively correlated with the presence of farm fields, human population density and distance to water, and positively correlated with log (transect length) and tracking conditions (Spearman rank tests; $P < 0.05$). The best multiple linear regression model of species richness ($R^2 = 0.42$) included human population density, tracking conditions and log (transect length); a competing model also included distance to water ($R^2 = 0.45$). Tracking conditions had the largest effect ($\Sigma w_i = 0.95$), followed by human population density ($\Sigma w_i = 0.73$), distance to water ($\Sigma w_i = 0.54$) and log (transect length) ($\Sigma w_i = 0.50$). Competing best models for the number of species with high detectability (> 0.7 for a single visit; Table S1) outside of protected areas included human population density, elevation, tracking conditions and log(transect length) ($R^2 = 0.54–0.58$).

Accounting for unequal detectability

We had sufficient data to estimate detectability for 32 species; 20 of those species had high detectability ($P_{det} > 0.7$; Table S1). True detectability was probably higher given that the year-long interval between site visits likely violated closure assumptions. Of candidate focal species, point estimates of detectability (P_{det}; Table S1) between years on repeated transects were highest for elephant ($P_{det} = 1$), high for hyaena ($P_{det} = 0.83$), variable for ungulates, and low for leopard ($P_{det} = 0.33$). Strong correlation of species counts on repeated transects for all large mammals (Spearman rank test, $r_s = 0.81$, $P < 0.0001$), ungulates ($r_s = 0.71$, $P = 0.0015$) and carnivores ($r_s = 0.71$, $P = 0.0014$) suggested that estimates of species richness were relatively consistent between years. Elephant presence was highly correlated with the restricted subset of highly detectable species, and model selection of richness of highly detectable species included similar variables

Table 3 Correlation of elephant presence with other large mammals in the study area, as determined by Spearman rank tests and pairwise correlation with degrees of freedom modified to account for spatial autocorrelation (Dutilleul, 1993).

Transect location and number (n)	Variable	Spearman r_s	P	Corrected d.f.	Corrected P
All transects ($n = 63$)	All species (excepting elephants)	0.50	< 0.0001	42	0.001
	Ungulates	0.56	< 0.0001	41	< 0.001
	All carnivores	0.43	< 0.0001	43	< 0.003
	Large carnivores*	0.50	< 0.0001	52	< 0.001
	Mammals > 45 kg	0.59	< 0.0001	43	< 0.001
	Species tolerating human activity†	−0.06	0.633	50	0.845
	Species with probability of detection > 0.7 ($n = 20$)	0.52	< 0.0001	41	< 0.001
	Species with probability of detection > 0.9 ($n = 5$)	0.79	< 0.0001	36	< 0.001
Village lands and Game Controlled Areas ($n = 40$)	All species (excepting elephants)	0.52	< 0.001	32	< 0.001
	Ungulates	0.47	0.002	37	0.002
	All carnivores	0.53	< 0.001	29	0.002
	Large carnivores*	0.41	0.009	33	0.018
	Mammals > 45 kg	0.58	< 0.001	38	< 0.001
	Species tolerating human activity†	0.21	0.195	36	0.136
	Species with probability of detection > 0.7 ($n = 20$)	0.57	< 0.001	32	< 0.001
	Species with probability of detection > 0.9 ($n = 6$)	0.85	< 0.0001	25	< 0.001

*Lion Panthera leo, spotted hyaena Crocuta crocuta, leopard Panthera pardus, wild dog Lycaon pictus, cheetah Acinonyx jubatus.
†Yellow baboon, hare species, cane rat, African civet, genet species, mongoose species, vervet monkey.

in the best models to those selected in the full analysis (Table 2).

Visualizing connectivity across the study area

Circuit-theoretic maps of current for nine species showed that potential connectivity varied widely among species but areas of high potential connectivity for elephants corresponded with higher connectivity for other species (Fig. 2). Species such as giraffe (Giraffa camelopardalis) and lion that were largely restricted to protected areas showed low potential connectivity, but the opposite was observed for elephant, greater kudu (Tragelaphus strepsiceros), spotted hyaena and other species. Impala likely were restricted by habitat preferences but showed correspondence with areas of high potential elephant connectivity where they occurred (Fig. 2a,d).

DISCUSSION

We detected elephant activity at adjacent survey locations spanning most of the study area (Fig. 1), implying that gene flow, if not movement across the entire linkage by individual elephants, could still link elephant populations in the critically important reserve complexes of the Ruaha and Selous ecosystems. The strong association of elephants with other large mammal species inside and outside reserves (Table 3; Fig. 2) and the negative association of human population density with elephants and mammal richness (Tables 1 and 2) suggest that African elephants are a reliable focal species for many large

mammals in this region. Highly specialized or sensitive species such as cheetah and wild dog do not appear to be appropriate focal species at this scale because they were never detected outside of protected areas during our study. While Williams et al. (2000) found that elephants and other large mammals were poor surrogates for mammals and bird diversity at large scales across sub-Saharan Africa, the much finer spatial scale of our study, restricted diversity and different evaluation criteria may explain our different findings.

The generality of our findings will likely depend on the spatial scale of examination. Multi-species linkages across landscapes must allow both movements by passage species and gene flow for resident (dispersal limited) species that persist within the linkage (Beier et al., 2008). While elephants may be one of the few potential 'passage' species at the scale of this linkage, extensive dry- and wet-season sign clearly indicated widespread and prolonged elephant activity in some areas. The strong patterns of co-occurrence we detected demonstrate that those areas provide habitat and likely allow gene flow for many other large mammal species (Table 3; Fig. 2). However, our field observations and discussions with villagers suggested that elephants sometimes used very specific paths when moving between local centres of activity, and the association with other mammal species along those paths is unclear. Thus, elephants may best serve as focal species for linkage planning at regional rather than local scales.

Protected area status and human population density were the strongest correlates with elephant occurrence (Tables 1 and 2), as expected, given the history of elephant killing for meat
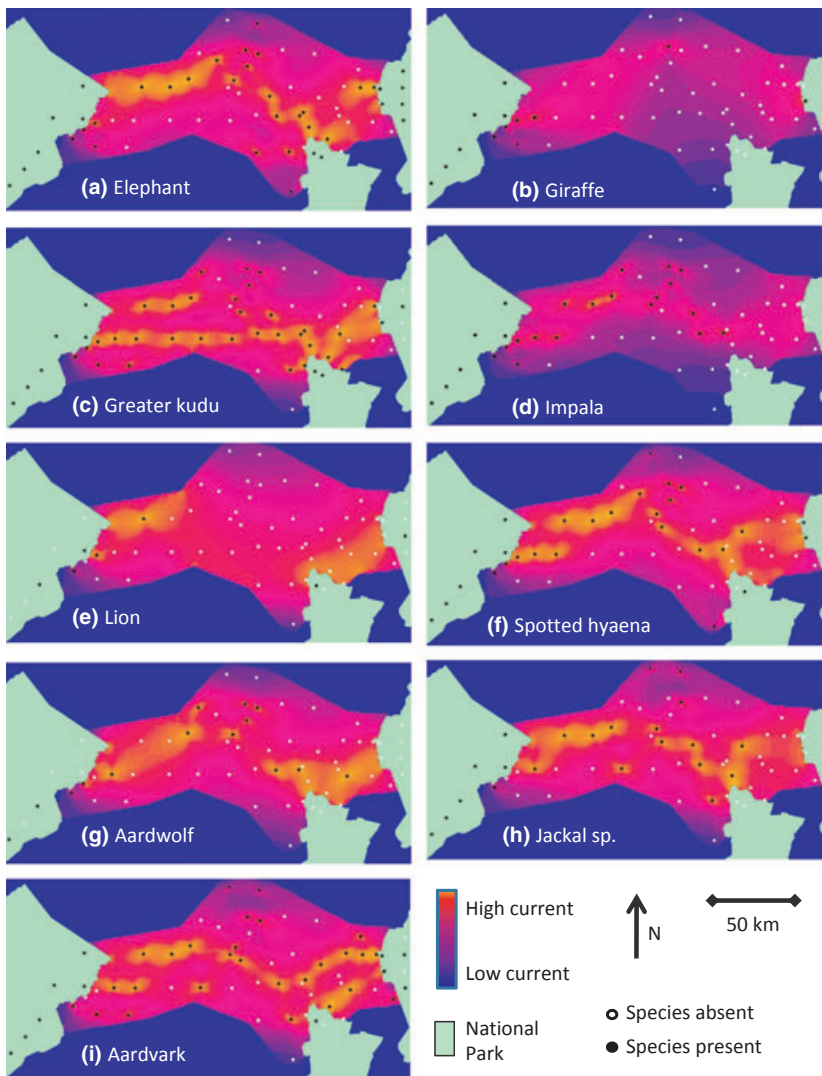
Figure 2 Circuit-theory modelling of 'current' between three reserves (except giraffe and impala; two reserves) based on species occurrence for elephants and eight other species selected from those with detectability > 0.65. Warmer colours (yellow-orange) depict higher probability of a given cell being used by a random-walk model of movement between nodes (reserves) based on a resistance surface defined, for each species, as distance from the nearest transect where that species was detected.

and ivory in central Tanzania (Gobush *et al.*, 2009). However, we detected elephants at many locations far from regularly patrolled protected areas (Fig. 1) and sometimes near human settlements. Some areas with widely reported histories of elephant movements within the last decade exhibited no recent sign or reports of elephants; local people often blamed conflicts associated with increased settlement and agriculture. Elephants were active across the study area in both wet and dry seasons and used some mountainous areas despite being detected more often at lower elevations (Table 2).

Strong heterogeneity in habitat and human activity has allowed many species to persist outside reserves (Fig. 1; Appendix S2), including species such as giraffe that are very vulnerable to illegal hunting. However, we encountered extensive evidence of hunting across the study area (snares, gunshots, etc.), and village scouts often reported heavy harvest and sharp declines (e.g. of buffalo, giraffe and impala *Aepyceros melampus*) or extirpation (e.g. of zebra *Equus quagga* east of the Idodi-Pawaga WMA, Fig. 1) of some species. Large ungulates are often favoured and highly vulnerable targets

for bushmeat hunting (e.g. Fa *et al.*, 2005; Laurance *et al.*, 2006; Ndibalema & Songorwa, 2008), and large carnivores are likewise vulnerable if the prey base declines or they are killed by humans because of livestock predation (e.g. Gusset *et al.*, 2009). Lion, cheetah, wild dog, zebra, eland (*Taurotragus oryx*), roan antelope (*Hippotragus equinus*), wildebeest (*Connochaetes taurinus*) and Grant's gazelle (*Gazella granti*) were never or almost never (in the case of lion) detected outside protected areas (Appendix S2). Although habitat differences may explain some of those absences, local people in some areas claimed that species such as lion, zebra and wild dog were once commonly seen. Thus, we argue that human activity is the primary driver of the geographic patterns we observed.

The focal species approach to linkage conservation may be most attractive where, as in our study area, detailed habitat data are unavailable but focal species are highly detectable. Presence of elephants and other focal species predicted large mammal richness better than our best multivariate habitat models. Of potential focal species, elephants were most easily detected. Thus, for both biological and social reasons,

elephants appear to be an ideal species to help guide conservation efforts for the diverse community of large terrestrial mammals in our study area. Interest in conserving wildlife corridors, particularly for elephants, has grown rapidly in Tanzania in recent years as human conflict with elephants has increased in scale and intensity (Caro *et al.*, 2009; Jones *et al.*, 2009). Wildlife corridors are sometimes controversial because they may be perceived by local people as a 'land grab' (Goldman, 2009), but a linkage design that specifically addressed human–elephant conflicts could benefit local people and biodiversity.

Although potential connectivity among reserves clearly varies widely with species-specific habitat and dispersal preferences (Fig. 2), our findings suggest that the conservation of elephant corridors will help maintain stepping-stone habitat and connectivity among protected areas for many other species of large terrestrial mammals in East Africa. A fully realized linkage design should consider species-specific habitat preferences, appropriate scales for movement and gene flow, and the representation of other biodiversity not evaluated here (e.g. small mammals, birds, reptiles, insects, plants). However, given that Tanzania and other countries are pushing forward with corridor conservation, employing focal species with demonstrated local applicability for linkage designs may be a practical first step when time and resources for conservation efforts are highly constrained.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Detailed protocol for walking transects and track sampling.

Appendix S2 Species detected during transect sampling.

Table S1 Detection probabilities estimated using PRESENCE.

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