Journal of Applied Ecology

British Ecological Society

Journal of Applied Ecology 2016, **53,** 1225–1235 doi: 10.1111/1365-2664.12650

Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community

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Summary

1. Emerging conservation paradigms have shifted from single to multi-species approaches focused on sustaining biodiversity. Multi-species hierarchical occupancy modelling provides a method for assessing biodiversity while accounting for multiple sources of uncertainty.

2. We analysed camera trapping data with multi-species models using a Bayesian approach to estimate the distributions of a terrestrial mammal community in northern Botswana and evaluate community, group, and species-specific responses to human disturbance and environmental variables. Groupings were based on two life-history traits: body size (small, medium, large and extra-large) and diet (carnivore, omnivore and herbivore).

3. We photographed 44 species of mammals over 6607 trap nights. Camera station-specific estimates of species richness ranged from 8 to 27 unique species, and species had a mean occurrence probability of 0·32 (95% credible interval = 0·21–0·45). At the community level, our model revealed species richness was generally greatest in floodplains and grasslands and with increasing distances into protected wildlife areas.

4. Variation among species' responses was explained in part by our species groupings. The positive influence of protected areas was strongest for extra-large species and herbivores, while medium-sized species actually increased in the non-protected areas. The positive effect of grassland/floodplain cover, alternatively, was strongest for large species and carnivores and weakest for small species and herbivores, suggesting herbivore diversity is promoted by habitat heterogeneity.

5. *Synthesis and applications*. Our results highlight the importance of protected areas and grasslands in maintaining biodiversity in southern Africa. We demonstrate the utility of hierarchical Bayesian models for assessing community, group and individual species' responses to anthropogenic and environmental variables. This framework can be used to map areas of high conservation value and predict impacts of land-use change. Our approach is particularly applicable to the growing number of camera trap studies world-wide, and we suggest broader application globally will likely result in reduced costs, improved efficiency and increased knowledge of wildlife communities.

Key-words: biodiversity, body size, camera trap, diet, grasslands, hierarchical Bayesian models, human disturbance, multi-species modelling, protected areas, species richness

Introduction

Prioritizing conservation actions, quantifying the impacts of management decisions and designating protected areas are just a few of the challenging tasks faced by wildlife managers and conservationists. To address these tasks, surrogate species are often used (Carroll, Noss & Paquet 2001; Epps *et al.* 2011) such that by focusing on the requirements of the surrogate, the needs of an entire community are addressed (Lambeck 1997). This concept, however, is widely debated given that actions aimed at

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conserving a single species have positive and negative effects on a wealth of other non-target species (Simberloff 1998; Wiens *et al.* 2008). As a result, emerging conservation and management paradigms favour multi-species vs. single species approaches where the objective is sustaining biodiversity and ecosystem functions (Yoccoz, Nichols & Boulinier 2001; Balmford *et al.* 2005).

Multi-species hierarchical occupancy models (Dorazio & Royle 2005), a recent advancement in community modelling, can be used to evaluate the spatial ecology of wildlife communities. As occupancy models (MacKenzie *et al.* 2002), they account for imperfect detection using temporally or spatially replicated data collected in a time period during which populations are assumed to be geographically closed. As hierarchical models, they integrate data across species, permitting composite analyses of communities, species groups and individual species (Russell *et al.* 2009; Zipkin, DeWan & Royle 2009). Sharing data across species leads to increased precision in estimates of species richness and species-specific occupancy, particularly for rare and elusive species (Zipkin *et al.* 2010). Multi-species hierarchical models can also be parameterized with variables hypothesized to influence the distributions of wildlife, allowing evaluation of how these variables affect wildlife communities, groups of species or a species of concern (Russell *et al.* 2009).

The spatial ecology of wildlife is often shaped by human disturbance. Increasing human populations and the corresponding demand for land has resulted in land-use change, fragmentation and infrastructure development being some of the greatest threats to biodiversity (Alkemade *et al.* 2009). One of the most prevalent forms of land-use change is conversion of wildlands to agriculture. Agricultural expansion has resulted in losses of 20–50% of forested land and 25% of grasslands globally (DeFries, Foley & Asner 2004). To combat the loss of wildlands and associated biodiversity, 12·7% of the Earth's land area has been designated as protected (Bertzky *et al.* 2012). The success of conserving biodiversity in these protected areas, however, is mixed (Western, Russell & Cuthill 2009; Craigie *et al.* 2010; Kiffner, Stoner & Caro 2013). In Kenya, for example, wildlife has declined at similar rates inside and outside of protected areas (Western, Russell & Cuthill 2009), whereas in Tanzania, species within protected areas fare better (Stoner *et al.* 2007). Land-use change may also lead to construction of artificial barriers such as roads and fences which can alter animal movements and fragment ecosystems (Forman & Alexander 1998; Hayward & Kerley 2009). The impacts of roads on wildlife vary widely, with increased human and vehicle activity often leading to increases in road mortality, edge effects and both legal and illegal hunting pressure (Forman & Alexander 1998). The impact of fences, in contrast, depends on the type of fence and purpose (Hayward & Kerley 2009). Fences can minimize threats from humans and domestic animals but if erected with little regard to wildlife movements, the result can be mass mortality of migrating ungulates (Hayward & Kerley 2009).

The spatial ecology of wildlife is also shaped by environmental features such as access to water, food availability and vegetation cover. For example, occupancy of mammals often declines with increasing distance to permanent water (Pettorelli *et al.* 2010; Epps *et al.* 2011; Schuette *et al.* 2013). Mesic habitats such as seasonal floodplains, however, tend to be characterized by relatively tall, less nutritious grass species (Hopcraft *et al.* 2012), which could result in grazing species preferring areas further from permanent water. The influence of vegetation cover, alternatively, is likely to be species specific (Estes 1991). Within the African carnivore guild, for example, black-backed jackals *Canis mesomelas* often avoid floodplains and grasslands (Kaunda 2001), whereas servals *Leptailurus serval* prefer these land covers (Pettorelli *et al.* 2010; Schuette *et al.* 2013).

A species' response to ecological variables may also be influenced by their life-history traits. Theory suggests, for example, that larger-bodied species in trophic groups at the top of the food chain (e.g. large carnivores) are more likely to decline than lower trophic guild species under similar conditions (Gaston & Blackburn 1996; Davies, Margules & Lawrence 2000). Life-history characteristics of species at high trophic levels, including low population densities, high food requirements and large home ranges, make them particularly vulnerable to persecution and fluctuating environments (Gard 1984; Ripple *et al.* 2014). Large-bodied animals are also targeted by trophy hunters (Packer *et al.* 2009) and bushmeat hunters (Fa, Ryan & Bell 2005). Consequently, we would expect large-bodied species near the top of the food chain to show greater sensitivity to anthropogenic and environmental changes.

In this study, we explore the utility of camera trap surveys and multi-species hierarchical models to inform biodiversity management. We applied our multi-species approach to a community of mammals in the Okavango Delta, Botswana – a World Heritage Site that is home to abundant wildlife including some of Africa's most endangered mammals. Better understanding of the spatial ecology of the mammal community will allow managers to more fully balance gains against losses when managing the diversity of wildlife (Western, Russell & Cuthill 2009; Zipkin, DeWan & Royle 2009). Additionally, our research was motivated by the lack of broad-scale wildlife community studies. Community-level studies generally focus on a particular guild of species such as carnivores (Pettorelli *et al.* 2010; Schuette *et al.* 2013) or ungulates (Stoner *et al.* 2007; Western, Russell & Cuthill 2009; Kiffner, Stoner & Caro 2013). Our study is among the first to evaluate the distributions of all terrestrial mammals >0·5 kg, excluding rodents.

Our specific objectives were to quantify species richness, evaluate species' distributions and elucidate community, group, and species-specific responses to human disturbance and environmental variables. We hypothesized (i) species richness, group richness and species-specific occupancy would be inversely related to human disturbance with large-bodied wildlife and carnivores expected to show the strongest relationships (Epps *et al.* 2011; Hopcraft *et al.* 2012; Schuette *et al.* 2013) and (ii) environmental conditions related to occupancy, in comparison with human disturbance, would be unique to each species and have weaker community and group-level effects. Our research aims to provide a better understanding of how environmental features and anthropogenic pressures are impacting species' distributions in southern Africa. Additionally, our analysis framework is applicable to the growing number of camera trap studies world-wide and could be applied to various land-use-related activities including mapping areas of high conservation value, predicting the effects of human development and providing guidance for management strategies aimed at sustaining biodiversity.

Materials and methods

STUDY AREA

Our study was carried out in Ngamiland District of northern Botswana, where the Okavango Delta and the northern reaches of the Kalahari Desert are located. The area (*c.* 550 km^2; 19°31′S 23°37′E) included a mixture of floodplains/grasslands, acacia woodland savannas, mopane *Colophospermum mopane* shrub and woodlands, and mixed shrublands. Our study site included the eastern section of Moremi Game Reserve, wildlife management areas NG33/34 and part of the livestock grazing areas of Shorobe (Fig. 1). Wildlife was fully protected within Moremi Game Reserve and partially protected within the wildlife management areas under a policy known as community-based natural resource management (Mbaiwa, Stronza & Kreuter 2011). Both areas were primarily used for photographic tourism. Moremi, however, was open to self-drive tourists and safari companies, whereas the wildlife management areas were only accessible to Sankuyo community members and safari companies with leases in the area. Consequently, the game reserve had higher human activity ($\bar{x}$ = 6 vehicles per day per camera station) than the wildlife management areas ($\bar{x}$ = 2 vehicles per day per camera station). The wildlife management areas were separated from adjacent livestock grazing areas by an extensive 1·3-m high cable veterinary fence that was erected to prevent the transmission of foot-and-mouth disease from Cape buffalo *Syncerus caffer* to cattle (Keene-Young 1999). Carnivores and other wildlife species, however, commonly pass through the fence (Keene-Young 1999). Wildlife within the management and livestock areas could be legally killed when the animal posed a threat to human life or property (Republic of Botswana Conservation and National Parks Act 2001).

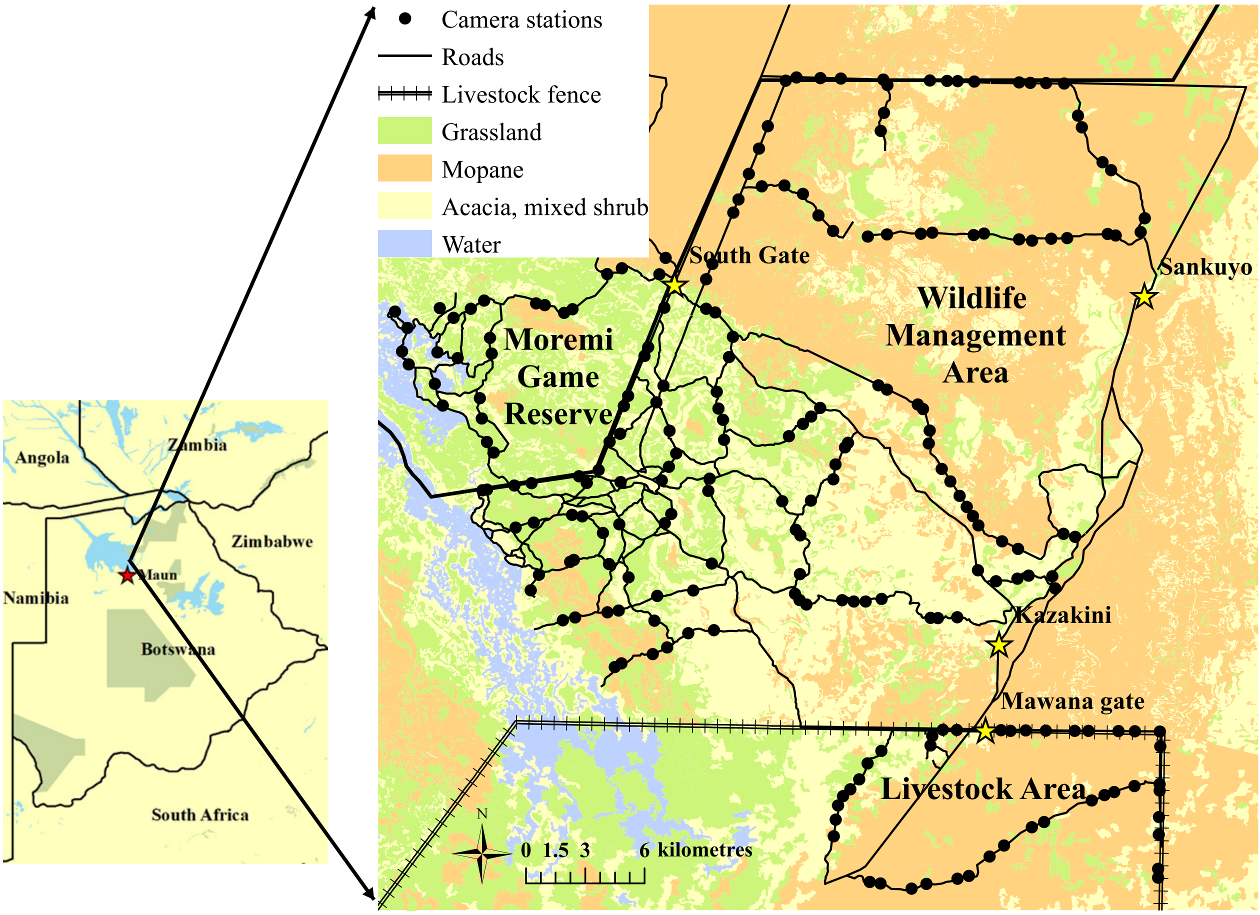

Fig. 1. Our study area including the eastern section of Moremi Game Reserve, wildlife management areas NG33/34 and livestock grazing areas in Shorobe, Botswana.

CAMERA TRAP SURVEY

We deployed Panthera v4 incandescent-flash and Bushnell Trophy Cam infrared camera traps at 221 locations across our 550-km^2 study area between February and July 2015 (Fig. 1). We used 5-km^2 grid cells to guide the placement of cameras. To increase our probability of photographing wildlife, we placed cameras on sand roads because wildlife species including large predators, carrion feeders and small mammals often use lightly travelled roads as movement corridors (Forman & Alexander 1998). We deployed two camera stations within each grid cell, one on the road closest to the predetermined centre point of each grid cell and the second on the road closest to a predetermined random point within each grid cell. We used a rotational system for camera deployment. We divided our study area into five, ~110 km^2 subareas and sequentially sampled each area for 30 nights. We deployed an average of 44 camera stations (i.e. 88 cameras) within each subarea.

Each camera station included two opposing cameras mounted on trees. If there were no trees available, we mounted cameras on metal fence posts hammered into the ground. We secured cameras at knee height and positioned cameras to photograph flanks of passing animals. We programmed cameras to take three photographs when triggered in the day with a delay of 30 s between photograph events. At night-time, the infrared cameras took three photographs when triggered, but the flash cameras could only take one photograph every 15 s due to the flash having to recharge. We checked cameras every 5–10 days to download photographs, replace batteries and ensure cameras were operational.

COVARIATES

We hypothesized the spatial distributions of wildlife may be influenced by two measures of human disturbance: human/vehicle capture rate and distance into the wildlife area. We did not include distance to human development as the majority of human development was concentrated in the livestock area. To calculate human/vehicle capture rate, we determined the mean number of photograph events of humans travelling by foot, donkey, horse and vehicles per trap night for the respective camera station. Next, in ArcMap 10.3.1 (ESRI, Redlands, CA, USA), we calculated distance into the wildlife area as the distance (km) from each camera station to the veterinary fence that separated wildlife and livestock areas. For camera stations within the livestock area, we gave distances a negative value to reflect how far removed they were from the wildlife area.

In addition to human disturbance, we hypothesized environmental variables including vegetation cover and distance to water may influence spatial distributions of wildlife. To quantify vegetation cover, we used a habitat map created by Bennitt, Bonyongo & Harris (2014). The dominant vegetation cover included floodplains/grasslands and mopane shrub and woodlands. For each of these vegetation covers, we calculated percentage cover within a 1-km buffered area surrounding each camera station. A 1-km buffer size provides information on the general conditions surrounding the camera station applicable to our suite of variably sized species. Floodplains/grasslands and mopane were highly correlated (Pearson $r = -0{\cdot}76$) so we only retained floodplains/grasslands for our analyses. We estimated distance to water by calculating the distance (km) from each camera station to the nearest permanent water source including rivers, ponds, lagoons and large pans. We were unable to account for seasonal water sources.

Finally, we hypothesized human/vehicle capture rate, road density and vegetation density may influence a species' probability of being photographed. To calculate road density, we georeferenced all roads and calculated road density for the area immediately surrounding each camera station (i.e. 250-m buffered area) in ArcMap. To measure vegetation density around camera stations, we took two photographs at knee height, pointed at 90° and 270° in relation to the road. We took these photographs at the camera station, 50 m up the road and 50 m down the road for a total of six photographs per station. We then digitally placed a 13 × 15 grid over each photograph and counted the number of grid cells that were ≥50% covered by forbs, shrubs or trees. We divided this count by the total number of grid cells and used the mean value across the six photographs as our estimate of vegetation density for the respective camera station.

MODELLING FRAMEWORK

We used multi-species hierarchical occupancy modelling (Dorazio & Royle 2005) to estimate the probability species i occurred within the area sampled by a camera station during our survey period (i.e. occurrence), while accounting for incomplete detection (MacKenzie *et al.* 2002). Specifically, we defined occurrence, $z_{i,j}$, as a binary variable where $z_{i,j} = 1$ if camera station j was within the range occupied by species i and 0 otherwise. We assumed $z_{i,j}$ was a Bernoulli random variable, $z_{i,j} \sim \text{Bern}(\psi_{ij})$, where ψ_{ij} is the probability that species i occurred at camera station j. Distinguishing the true absence of a species from the non-detection of a species (i.e. species present but not photographed) requires spatially or temporally replicated data. We treated each trap day as a repeat survey at a particular camera station resulting in ~30 sampling occasions per camera station. We estimated the probability of observing species i at camera station j on trap day k conditional on the site being occupied as $\text{x}_{i,j,k} \sim \text{Bern}(p_{i,j,k} * z_{i,j})$ where $p_{i,j,k}$ was the detection probability of species i at camera station j during trap day k, given that species i was truly present at camera station j (MacKenzie *et al.* 2002).

We incorporated site-level characteristics affecting species-specific occurrence and detection probabilities using a generalized linear mixed modelling approach (Dorazio & Royle 2005; Russell *et al.* 2009). We followed the protocol of Zipkin, DeWan & Royle (2009) and Zipkin *et al.* (2010) of fitting a single model with a limited number of covariates for which there was a strong *a priori* justification. The occurrence probability for species i at camera station j was specified as:

$$\begin{aligned}\text{logit}(\Psi_{ij}) = {} & \alpha0_i + \alpha1_i(\text{human/vehicle trap rate})_j \\ & + \alpha2_i(\text{wildlife area})_j + \alpha3_i(\text{floodplains/grasslands})_j \\ & + \alpha4_i(\text{water})_j,\end{aligned}$$

and detection probability as:

$$\begin{aligned}\text{logit}(p_{ij}) = {} & \beta0_i + \beta1_i(\text{road density})_j + \beta2_i(\text{vegetation density})_j \\ & + \beta3_i(\text{human/vehicle trap rate})_j\end{aligned}$$

We standardized all covariates to have a mean of 0 and standard deviation of 1. Therefore, the inverse logit of $\alpha0_i$ and $\beta0_i$

are the occurrence and detection probabilities, respectively, for species i at a camera station with average covariate values. Remaining coefficients ($\alpha 1_i$,.., $\alpha 4_i$, and $\beta 1_i$,..,$\beta 3_i$) represent the effect of a one standard deviation increase in the covariate value for species i. A species' abundance can significantly affect detection probabilities, often resulting in strong, positive correlations between occupancy and detection (Royle & Nichols 2003). As a result, we modelled among species correlation (ρ) between $\alpha 0_i$ and $\beta 0_i$ by specifying the two parameters to be jointly distributed (Dorazio & Royle 2005; Kéry & Royle 2008).

We linked species-specific models using a mixed modelling approach. We assumed species-specific parameters were random effects derived from a normally distributed, community-level hyper-parameter (Zipkin *et al.* 2010). Hyper-parameters specify the mean response and variation among species within the community to a covariate (Kéry & Royle 2008). Specifically, for our community model, the α coefficients were modelled as $\alpha_i \sim$ normal(μ_α, $\sigma^2{}_\alpha$) where μ_α is the community-level mean and $\sigma^2{}_\alpha$ is the variance (Chandler *et al.* 2013). We also hypothesized body size and diet may influence how a species responds to the respective covariates. Thus, we divided species into body size groups based on mean body mass for males and females (Estes 1991). Groups included extra-large (≥200 kg)-, large (50–200 kg)-, medium (20–50 kg)- and small (<20 kg)-sized species (see Appendix S1, Supporting information). The diet groups included carnivores, herbivores and omnivores (Estes 1991). To assess group-level effects, we allowed α coefficients to be species-specific and governed by a group-level and community-level hyper-parameter. For our group models, α coefficients were modelled as functions of the community-level mean, group-level mean (body size or diet group) and species-specific effect for the respective covariate.

We estimated posterior distributions of parameters using Markov chain Monte Carlo (MCMC) implemented in JAGS (version 3.4.0) through program R (R2Jags; Plummer 2011). We generated three chains of 50 000 iterations after a burn-in of 10 000 and thinned by 50. For priors, we used a uniform distribution of 0 to 1 on the real scale for $\alpha 0_i$ and $\beta 0_i$ and uniform from 0 to 10 for σ parameters. We used a normal prior distribution with a mean of 0 and standard deviation of 100 on the logit-scale for the remaining covariate effects ($\alpha 1_i$,.., $\alpha 4_i$ and $\beta 1_i$,..,$\beta 3_i$). We assessed convergence using the Gelman–Rubin statistic where values <1·1 indicated convergence (Gelman *et al.* 2004).

During each iteration, the model generates a matrix of camera station and species-specific z values (i.e. an occupancy matrix) where as previously stated, $z_{i,j} = 1$ if camera station j was within the range occupied by species i and 0 otherwise. To estimate species richness at camera station j, we summed the number of estimated species (i.e. instances where $z_i = 1$ for camera station j) during iteration x. We then repeated this process for each of the 50 000 iterations and used these values to generate a probability distribution representing camera station-specific species richness (Zipkin *et al.* 2010). We calculated group-level richness similarly, the only difference being that we restricted the estimate to species belonging to the respective group. As an example, the complete specification for the diet group model and how we calculated species and group richness is presented in Appendix S2.

Results

We recorded 8668 detections of 44 species of mammals during our 6607 trap nights. Body size groups included 12 small, 11 medium, 11 large and 10 extra-large species (Appendix S1). Diet groups included 21 carnivores, 18 herbivores and 5 omnivores (Appendix S1). Brown hyaenas *Hyaena brunnea* ($n = 3$) and cheetahs *Acinonyx jubatus* ($n = 3$) were photographed least often, while African elephants *Loxodonta africana* ($n = 1665$) and impalas *Aepyceros melampus* ($n = 900$) were photographed most often.

COMMUNITY-LEVEL AND GROUP-LEVEL SUMMARIES

Our camera station-specific estimates of species richness ranged from 8 (95% credible interval = 5–12) to 27 (95% CI = 24–32) unique species (Appendix S3), with a mean of 17 (95% CI = 14–20). Species richness was generally greater in the game reserve ($\bar{x}$ = 20, 95% CI = 17–24) and wildlife management area ($\bar{x}$ = 17, 95% CI = 14–21) than within the livestock grazing area ($\bar{x}$ = 13, 95% CI = 10–16). Overall, species had lower detection probabilities in areas with high road density, vegetation density and human/vehicle trap rates (Table 1). Between the human disturbance variables, distance into the wildlife area had the largest impact on community-level species richness, with richness increasing as the camera station's distance into the wildlife area increased (Table 1; Fig. 2). This positive relationship was most evident for small species, extra-large species and herbivores (Table 2; Fig. 2). Mean richness of medium-sized species (5–25 kg) and omnivores, conversely, increased in livestock areas (Table 2; Fig. 2).

Between the environmental variables, percentage cover of floodplains/grasslands had the greater impact on community-level species richness, with richness generally increasing as floodplain/grassland cover increased (Table 1; Fig. 2). Floodplains/grasslands had the strongest influence on richness of large species followed by carnivores and omnivores, and the weakest influence on richness of small species and herbivores (Table 2; Fig. 2). The richness of all species groups was only weakly related to the camera station's distance from permanent water (Tables 1 and 2). Among these relationships, distance to permanent water had the largest influence on richness of extra-large species and omnivores with richness increasing closer to permanent water (Table 2). The 95% CIs for community-level and many group-level covariate effects overlapped zero (Tables 1 and 2), suggesting high variability among species and species groups. This result was not unexpected, given the diversity of species. Gelman–Rubin statistics indicated convergence for all parameters.

SPECIES-LEVEL SUMMARIES

The mean probability of occurrence across all species and camera stations was 0·32 (95% CI = 0·214–0·451), but this varied dramatically among species, ranging from 0·97 for elephants to 0·04 for brown hyaenas and cheetahs. Daily detection probabilities also varied greatly among

Table 1. Mean ($\bar{x}$) and 95% credible interval (95% CI) estimates of the community-level hyper-parameters hypothesized to influence the probability of use (α) and detection (β) of 44 mammal species in northern Botswana, 2015

Community-level hyper-parameter		$\bar{x}$	95% CI	
$\alpha1_i$	Human/vehicle trap rate	0·19	−0·049	0·489
$\alpha2_i$	Dist. into wildlife area	0·27	−0·002	0·547
$\alpha3_i$	Floodplain/grassland	0·16	−0·142	0·439
$\alpha4_i$	Dist. to permanent water	−0·02	−0·133	0·092
$\beta1_i$	Road density	−0·06	−0·142	0·015
$\beta2_i$	Vegetation density	−0·16	−0·247	−0·066
$\beta3_i$	Human/vehicle trap rate	−0·05	−0·134	0·019

species, ranging from 0·01 to 0·27. Variation among species in occurrence and detection probabilities was correlated, so that species occurring more widely were photographed on a greater proportion of days at individual camera stations ($\rho = 0{\cdot}39$, 95% CI = 0·126–0·882). Species-specific estimates of occurrence, detection and covariate effects are presented in Appendix S1.

Of the 44 species photographed, 20 were strongly (i.e. 95% CI did not overlap zero) related to distance into the wildlife area (14 positively and 6 negatively) and 23 to percentage cover of floodplain/grassland (15 positively and 8 negatively; Fig. 3). In contrast, occurrence of only seven and one species were strongly related to the trapping rate of humans/vehicles and distance to permanent water, respectively (Appendix S1). As expected, precision of estimates was lower for species with limited numbers of detections, leading to diffuse posterior distributions for their estimates of covariate effects.

Discussion

Our research highlights the importance of protected areas and grasslands in maintaining biodiversity in southern Africa (Millennium Ecosystem Assessment 2005; Biggs *et al.* 2008; Craigie *et al.* 2010). We found overall species richness was generally greater in floodplains and grasslands and areas located further into protected wildlife areas (Table 1; Fig. 2). Our results support regional conservation initiatives focused on grasslands as this biome is vulnerable to future land-use pressures (Biggs *et al.* 2008) and benefits a broad diversity of species, including large-bodied animals that are often threatened by hunting pressure (Fa, Ryan & Bell 2005; Packer *et al.* 2009). Additionally, over a quarter of the world's grasslands have already been lost (DeFries, Foley & Asner 2004) and the remaining grasslands are threatened by woody encroachment (Ratajzak, Nippert & Collins 2012). Our results also highlight the importance of protected wildlife areas, particularly to small- and large-bodied species, herbivores and carnivores. While the effectiveness of protected areas is mixed (Western, Russell & Cuthill 2009; Craigie *et al.* 2010; Kiffner, Stoner & Caro 2013), we found that livestock areas had lower levels of species richness and that species richness increased with distance into protected areas. These results are consistent with the trend of agriculture growth and habitat loss functioning as primary threats to biodiversity world-wide (Millennium Ecosystem Assessment 2005).

In northern Botswana, wildlife and livestock areas are separated by the veterinary fence. The fence is permeable to many species (e.g. carnivores) but impermeable or semipermeable to others. When the fences were erected, they cut-off migratory routes of wildebeests *Connochaetes taurinus* and zebras *Equus burchelli* and disturbed the movement patterns of additional ungulate species (Hayward & Kerley 2009). If the fence, as a physical boundary, was the underlying cause of increased species richness in wildlife areas, then we would expect species richness to be nearly constant between the core and edge of wildlife areas (Kiffner, Stoner & Caro 2013). Our results showing species richness increasing with distance from the fence, however, (Fig. 2) suggest other spatial factors such as land use and human–wildlife conflict (e.g. poaching and retaliatory killings) are likely to be contributing drivers of this edge effect (Woodroffe & Ginsberg 1998). Results presented here suggest management of human activities on both sides of protected area borders is essential for minimizing edge effects (Woodroffe & Ginsberg 1998).

The weak effects of human/vehicle trap rates and water accessibility on community-level species richness were surprising (Table 1). The human/vehicle trap rate results likely reflect that most of our study area was used by tourists or tourism operators, all of whom seek out areas with abundant wildlife. This human disturbance may have had minimal impact on nocturnal species given that tourism activities were generally restricted to daylight hours (i.e. via Game Reserve permit rules). Distance to permanent water had a weak effect on species richness in this study, in contrast with other studies in Africa (Pettorelli *et al.* 2010; Epps *et al.* 2011; Schuette *et al.* 2013). We found wildlife to be more evenly distributed across the landscape in relation to water availability perhaps because (i) our study took place during the end of the wet season and beginning of the dry season when water was less of a limiting resource, (ii) we were unable to account for ephemeral water sources and (iii) selection of high quantities of grass in wet areas vs. grass with higher nutrition in dry areas is species dependent (Hopcraft *et al.* 2012).

In addition to community-level effects, our multi-species approach allowed us to evaluate how specific groups of species were influenced by human and environmental factors. If managers wish to focus their efforts on conserving herbivores, for example, our research suggests protected areas and heterogeneity in vegetation types promote herbivore diversity. Similar to overall species richness, we found herbivore richness increased with distance into wildlife areas (Table 2; Fig. 2). The influence of grassland and floodplain cover, however, was highly variable (Fig. 2). Species that are predominantly grazers, such as zebras and impalas, were more likely to use grasslands and floodplains where their food source was

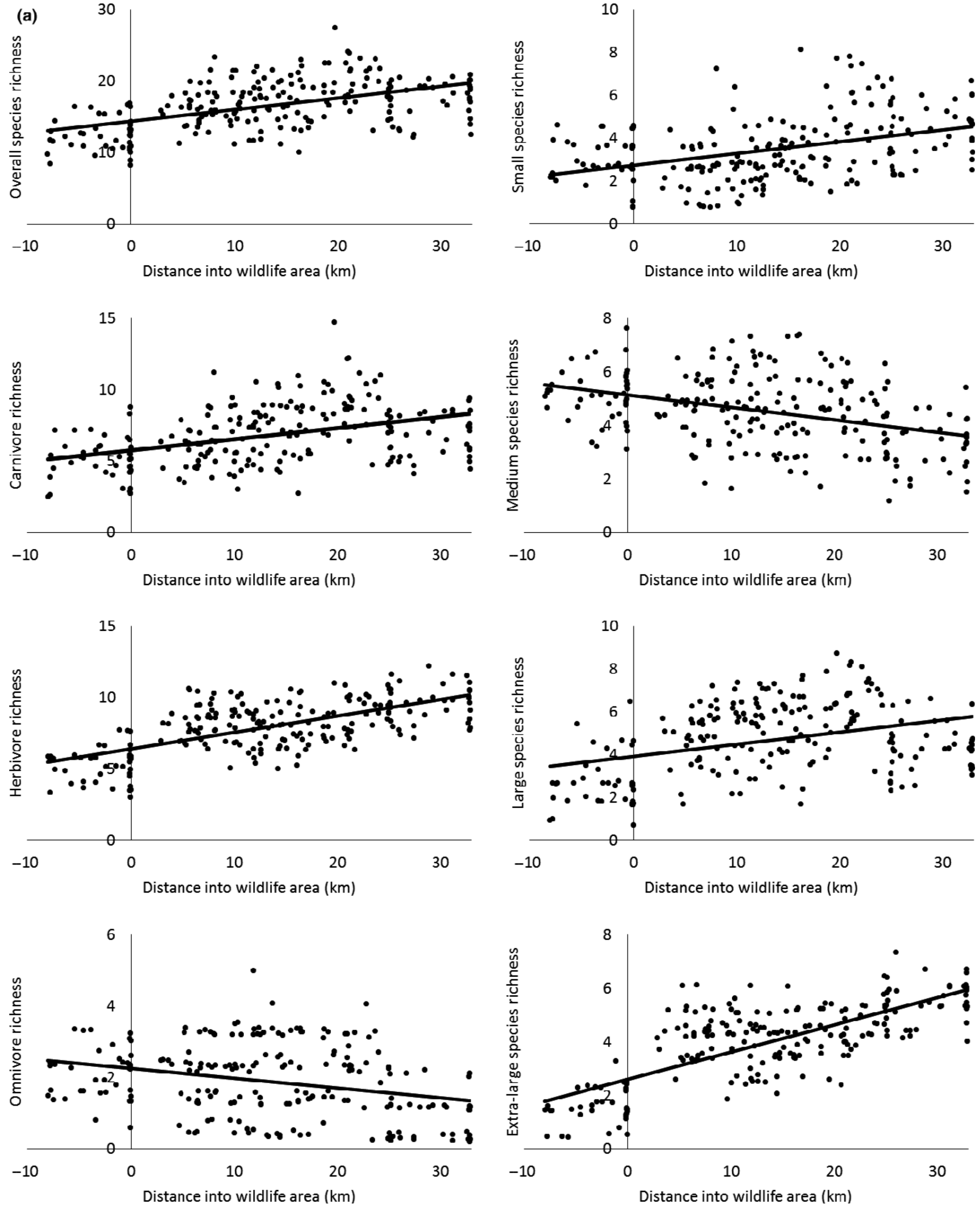

Fig. 2. Mean, site-specific estimates of overall species richness and the richness of diet and body size (small < 5 kg, medium 5–25 kg, large 25–200 kg and extra-large ≥ 200 kg) groups of species in relation to (a) the camera station's distance into a protected wildlife area (negative values indicate camera was in a livestock area) and (b) grassland/floodplain cover. Camera trap survey took place in Ngamiland District, Botswana, 2015.

abundant. We found small ungulates including steenbok *Raphicerus campestris* and bush duikers *Sylvicapra grimmia*, however, had a negative relationship with grasslands and floodplains. These small grazers may select for mixed shrub- and mopane-dominated areas because they are adapted to selecting high-quality components of grass

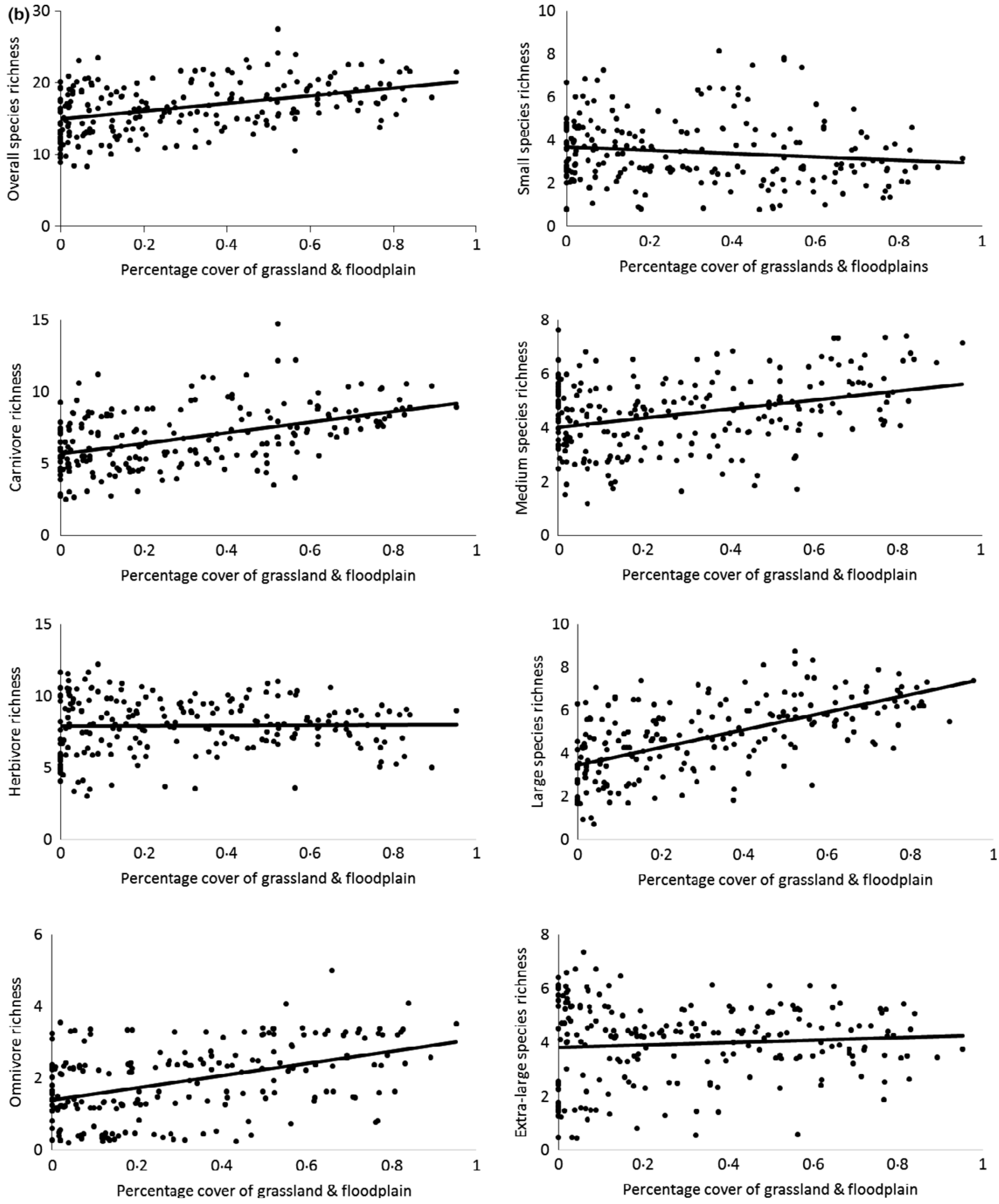

Fig. 2. Continued.

allowing them to forage in low biomass areas (Wilmshurst, Fryxell & Colucci 1999).

Our research can also be used to predict which groups of species or individual species would be most impacted by increasing levels of human disturbance in and outside of protected areas. As hypothesized, we found extra-large species like giraffes *Giraffa camelopardalis* and roan antelopes *Hippotragus equinus* were most sensitive to human disturbance where the probabilities of using an area increased with distance into the wildlife area (Table 2, Fig. 2). The groups of species that would likely be unaffected or positively affected by increasing levels of human disturbance were omnivores and medium-sized species (Fig. 2), such as the African civet *Civettictis civetta* and

Table 2. Mean ($\bar{x}$) and 95% credible interval (95% CI) estimates of the group-level hyper-parameters hypothesized to influence the probability 44 mammal species used the area sampled by our camera stations in northern Botswana, 2015. Body size groups included small (S = <5 kg), medium (M = 5–25 kg), large (L = 25–200 kg) and extra-large (XL = ≥200 kg) species and diet groups included omnivores (Omn), carnivores (Carn) and herbivores (Herb)

Body Size Group				Diet Group			
Group	$\bar{x}$	95% CI		Group	$\bar{x}$	95% CI	
Human/vehicle trap rate							
S	0·46	−0·035	1·127	Omn	0·59	−0·419	1·698
M	0·04	−0·472	0·659	Carn	0·38	−0·045	0·875
L	0·40	−0·112	1·067	Herb	0·02	−0·477	0·453
XL	−0·11	−0·831	0·441				
Distance into the wildlife area (km)							
S	0·36	−0·069	0·806	Omn	−0·43	−1·213	0·314
M	−0·31	−0·752	0·110	Carn	0·22	−0·166	0·582
L	0·21	−0·266	0·664	Herb	0·53	0·141	0·944
XL	0·90	0·410	1·398				
Floodplain/grassland (% cover)							
S	−0·07	−0·619	0·484	Omn	0·39	−0·444	1·244
M	0·18	−0·375	0·723	Carn	0·33	−0·111	0·751
L	0·64	0·052	1·220	Herb	−0·11	−0·575	0·333
XL	−0·17	−0·782	0·453				
Distance to water (km)							
S	0·16	−0·043	0·354	Omn	−0·27	−0·595	0·034
M	−0·09	−0·293	0·105	Carn	0·08	−0·090	0·247
L	−0·01	−0·220	0·223	Herb	−0·05	−0·216	0·133
XL	−0·19	−0·418	0·033				

jackal species (Fig. 3). Medium-sized omnivores tend to be generalists that can use a wide array of landscapes and thrive even after extensive human modification (Roemer, Gompper & Van Valkenburgh 2009).

Reliable methods for evaluating biodiversity are key to making informed conservation and management decisions (Pettorelli *et al.* 2010; Zipkin *et al.* 2010). Equally important is the need to understand how top-down (e.g. humans) and bottom-up (e.g. vegetation cover) factors influence diversity (Elmhagen & Rushton 2007). Our research demonstrates the utility of camera trap surveys and hierarchical models for assessing community, group and individual species' responses to both anthropogenic and environmental variables. Our study did, however, have some potential limitations. First, our sequential sampling of subareas may have violated the model's assumption of geographic closure (MacKenzie *et al.* 2002). A simulation study based on estimated occupancy and detection probabilities from our pilot season, however, found this sampling design balanced precision of occupancy estimates with survey effort. Secondly, because we only included camera station-specific covariates, we were unable to account for species-specific measures of predation and competition, which are known to influence species' distributions (Caro & Stoner 2003). Lastly, we sampled on sand roads to maximize detection probabilities (Forman & Alexander 1998). If cameras had been placed randomly, we believe the photographic rates of many wildlife species, particularly carnivores, would have been prohibitively low. However, if any species avoided roads, then our sampling design may have resulted in their true occupancy being underestimated.

Our multi-species approach provides a method for using detection/non-detection data to estimate and evaluate species' occupancy and richness that should reduce money, time and personnel costs, which are critical for many management agencies across the world where field data funding is limited (Zipkin, DeWan & Royle 2009). Camera trap surveys are an ideal field method for community studies on terrestrial species because they photograph every species that passes in front of them. Few studies, however, capitalize on this wealth of community information as attention is typically focused on a single species or guild of species (Stoner *et al.* 2007; Pettorelli *et al.* 2010; Schuette *et al.* 2013). Unlike traditional community analyses, our multi-species approach allowed us to retain species identity while properly accounting for multiple sources of uncertainty (Kéry & Royle 2008; Zipkin *et al.* 2010). Many of the species in our study had low detection probabilities which, if left unaccounted for, would have resulted in underestimates of species richness and affected estimates of our ecological variables (Zipkin *et al.* 2010). Additionally, our multi-species approach allowed us to integrate data across species using the community-level hyper-parameter (Dorazio & Royle 2005; Russell *et al.* 2009; Zipkin, DeWan & Royle 2009). This permitted us to complete a comprehensive assessment of all wildlife species and resulted in increased precision of species-specific occupancy probabilities, particularly for species that were rarely photographed. We suggest that broader application of this approach to camera trap studies world-wide will likely result in a more comprehensive and efficient use of available data and a better understanding of the spatial ecology of all species within the terrestrial wildlife community.

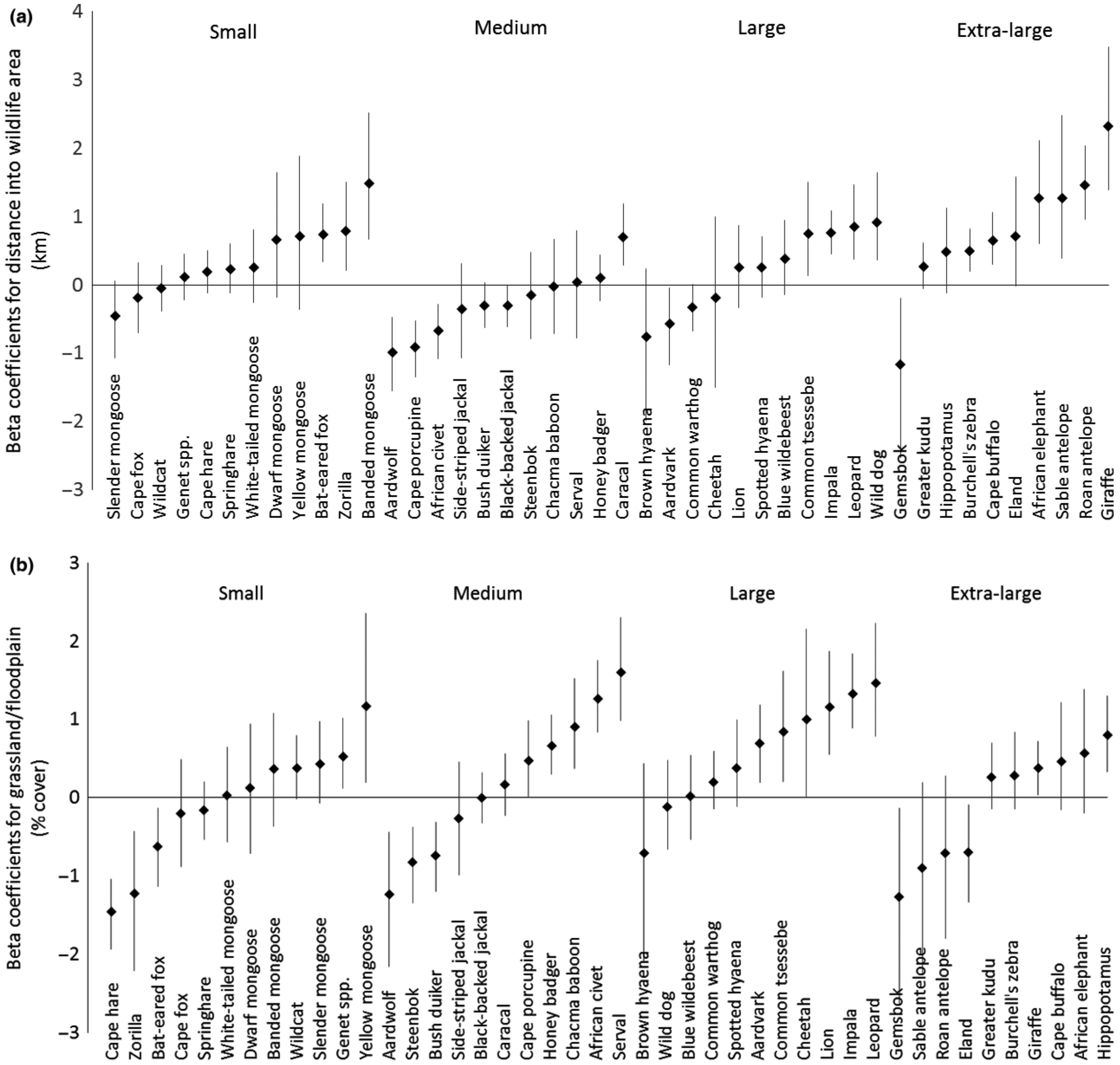

Fig. 3. Standardized beta (specified as α in model) coefficients, and 95% credible intervals, for the influence of distance into the wildlife area (a) and floodplain/grassland cover (b) on the probability a species used an area during our camera trap survey in northern Botswana, 2015. Species are arranged in body size groups including small (<5 kg), medium (5–25 kg), large (25–200 kg) and extra-large (≥200 kg).

Acknowledgements

We thank the government of Botswana, the Ministry of the Environment, Wildlife and Tourism, and the Department of Wildlife and National Parks for permission to conduct this study (permit EWT 8/36/4 XXIII 44). We thank K. Golabek, N. Jordan, L. Van der Weyde and R.H. Walker at BPCT for their assistance, R. Crous for permission to survey his property, A. Gabanakitso for help in the field and S.M. Karpanty and K.A. Alexander for feedback on the manuscript. This research was funded by a Fulbright Study/Research Grant, PEO Scholar Award, Wilderness Wildlife Trust, Columbus Zoo, Cleveland Metroparks Zoo, Wild Felid Association, Idea Wild, Temenos Foundation, The Rufford Foundation, Virginia Tech and the numerous donors who support the BPCT.

Data accessibility

Data available from the Dryad Digital Repository doi:10.5061/dryad.q54rp (Rich *et al.* 2016).

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Received 22 November 2015; accepted 11 March 2016
Handling Editor: Matt Hayward

Supporting Information

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

Appendix S1. Species-specific probabilities of occurrence, probabilities of detection and the effects of anthropogenic and habitat covariates.

Appendix S2. Hierarchical group model JAGS code.

Appendix S3. Camera station-specific estimates of species richness, including overall community, carnivore, omnivore, herbivore, small (< 5 kg), medium (5–25 kg), large (25–200 kg), and extra-large (> 200 kg) species richness.