



# Impact of land use on occupancy and abundance of terrestrial mammals in the Drakensberg Midlands, South Africa



Tharmalingam Ramesh, Colleen T. Downs\*

School of Life Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, Pietermaritzburg, KwaZulu-Natal 3209, South Africa

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## ABSTRACT

Better management and knowledge regarding the effect of land use intensification on mammal abundance and occupancy is crucial for species conservation. This is particularly true in dynamic forest-farmland mosaics subjected to rapid human-induced habitat alterations for agricultural practices. We conducted camera-trap surveys at 44 locations across farmland use gradients between October 2012 and January 2013. We estimated occupancy and relative abundance of 10 terrestrial mammals in response to farmland use in the Drakensberg Midlands, South Africa. Occupancy modelling revealed the importance of available forest and wetland to several mammals. Occupancy estimates for *Leptailurus serval* were lower in cropland than for *Herpestes ichneumon*, *Atilax paludinosus* and *Potamochoerus larvatus*. Occupancy of *Leptailurus serval* and *Redunca rundinu* increased with relative human abundance while the relationship was inverse for *Hystrix cristata* and *Potamochoerus larvatus*. Livestock-related activity influenced occupancy of *Potamochoerus larvatus* positively and *Hystrix cristata* negatively. Pesticide usage had a negative impact on detection of several mammals, and occupancy of *Atilax paludinosus*. Commercial plantation influenced occupancy of *Tragelaphus scriptus* and *Potamochoerus larvatus* positively. Plantation supported the abundance of five species positively. Wetland influenced relative abundance of *Leptailurus serval* positively. Pesticide use significantly decreased relative abundance of *Leptailurus serval* and *Atilax paludinosus*. Livestock and human relative abundance were positively associated with relative abundance of *Leptailurus serval* and *Canis mesomelas* and negatively for other species. Our models proved the sensitivity of some mammals towards the natural habitat loss due to agricultural practices while others appeared to be tolerant to such human-modified habitats. We suggest feasible management implications for conserving diverse mammalian assemblages in farmland mosaics.

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## Introduction

Land use changes that increase fragmentation and habitat loss pose a threat to terrestrial biodiversity (Jetz et al. 2007; Pereira et al. 2010). Changes that restrict traditional animal movements can lead to decline in species distribution and abundance (Msuha et al. 2012; Pimm & Raven 2000). Economic demands have led to land use changes which convert natural habitats into human-modified habitats, such as secondary forests and heterogeneous agricultural landscapes in tropical regions (Mulwa et al. 2012). Humans persuade habitat changes and are responsible for major biodiversity loss worldwide (Green et al. 2005; Kleijn et al. 2009; Sala et al. 2000). The impact of changes in land use practices on ecological communities is least known (Estes et al. 2011; Haines-Young 2009; Msuha et al. 2012). Consequences of structural changes of land

generally affect species diversity negatively (Blaum et al. 2007; Cingolani et al. 2005). Land use change, particularly, is of major concern in developing regions such as the Sub Saharan Africa, where human populations are expanding and the majority of people depend on natural resources for various livelihoods (Ceballos & Ehrlich 2006; Thuiller et al. 2006). Mammals are indicator species to study ecological disturbances such as structural changes of the landscape for conservation planning (Crooks 2002; Soule & Terborgh 1999; Woodroffe & Ginsberg 1998). Terrestrial mammals are an integral and valued part of land ecosystems. Understanding, how mammalian species respond to land use change provide important information for biodiversity conservation at the regional and global scale.

Historically, Protected Areas PA aimed to protect and maintain biological diversity and natural resources through legal means across the world (Naro-Maciel et al. 2009; Pressey 1996). While these areas may not provide sufficient protection for species residing outside PAs, some of them are too small to support long-term species survival (Naro-Maciel et al. 2009; Woodroffe and Ginsberg

\* Corresponding author. Tel.: +27 33 2605127/04; fax: +27 33 2605105.  
E-mail address: [downs@ukzn.ac.za](mailto:downs@ukzn.ac.za) (C.T. Downs).

1998). The persistence of mammals may depend on their survival outside PAs in southern Africa where they come into conflict with humans, and livestock (Kent 2011). Different carnivores may have a range of impacts on farmers (Kent 2011; Linnell et al. 1999). Farmland is the prevailing interface between mankind and nature, and has become a dominant form of land management around the world (Gall & Orians 1992; Gilpin et al. 1992). The intensification of farmland use has contributed to increase in production yields through technological advances by use of machinery, fertilizers and pesticides while it has a strong negative impact on biodiversity (Briggs & Courtney 1989).

If ecological integrity is to be maintained, priority should be given even in ecosystems surrounding PAs (Msuha et al. 2012; Newmark 1996; Woodroffe 2000), since they have the potential to hold significant populations of many wildlife species (Homewood & Rodgers 1991; Rowe-Rowe 1992). Studies have shown that increased intensity of land use reduces habitat and species diversity, distribution and abundance (Fitzherbert et al. 2008; Green et al. 2005; Maitima et al. 2009; Moreira & Russo 2007; Msuha et al. 2012; Wretenberg et al. 2010). Such intensification of land management typically reduces distribution and abundance of large sized ungulates and predators more than small sized ungulates and predators (Kinnaird and O'Brien 2012). Although some generalist species can show positive response to this change but territorial or habitat specialists may not sustain these changes. Effective biodiversity conservation can be achieved by understanding the level of relationship between terrestrial mammals and land-use intensity.

The farmlands of the Drakensberg Midlands in KwaZulu-Natal, South Africa are rangelands where humans, domestic livestock and wildlife coexist with varying degrees of success. The habitat types include montane grassland, wetland, patches of dense forest and bushland are being converted at large scale for agricultural purposes. A wide range of land management and livestock husbandry practices were apparent there (Pero & Crowe 1996). Knowledge regarding the impact of land use changes on many small and medium sized mammals is not well understood outside PAs (Pettorelli et al. 2010; Schipper et al. 2008). Species distribution and relative abundance are commonly used as state variables in evaluating the impact of different management interventions or anthropogenic disturbance on biodiversity (Kinnaird and O'Brien 2012; O'Brien 2008; Yoccoz et al. 2001). Camera trapping survey is considered as a better tool in determining abundance, occupancy, and habitat use of elusive species than other monitoring methods (Carbone et al. 2001; Ramesh et al. 2013; Tobler et al. 2009). Site occupancy can provide a reasonable estimate of population status in multi-species monitoring programs (Sarmiento et al. 2011). Consequently our study aimed to explore the response of terrestrial mammal occupancy and relative abundance to different land use practices in farmlands under single season occupancy modelling and Generalised Linear Models in the Drakensberg Midlands region of South Africa.

## Materials and methods

The amount of research conducted on commercial private farmland in South Africa is limited particularly in the province of KwaZulu-Natal (Rowe-Rowe 1992, 1994) and minority group that owns and manages these large areas of land. Our study was conducted in Fort Nottingham (Site A), Khamberg (Site B) and Mooi River (Site C) (29°41'–30°01' E, 29°10'–29°28' S) and for more detail see Ramesh and Downs (2013). Naturally occurring wild species include: common grey duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), blesbok (*Damaliscus dorcas*), common reedbuck (*Redunca arundinum*), oribi (*Ourebia ourebi*), bush buck (*Tragelaphus scriptus*), bush pig (*Potamochoerus larvatus*), vervet monkey

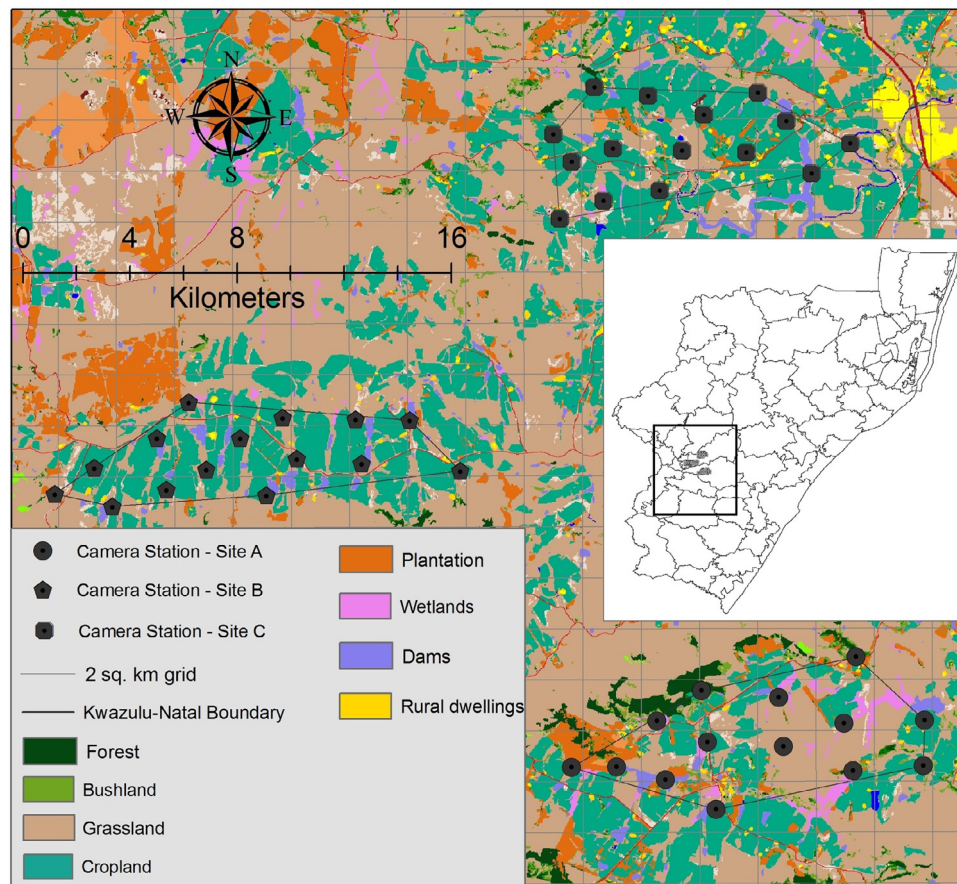
**Table 1**

The percent area availability of land use habitats according to land cover characteristics (Geoterralmage 2010) within the survey area of farmlands in the Drakensberg Midlands, KwaZulu-Natal, South Africa.

Habitat types	Site A	Site B	Site C
Highland Sourveld	45	12	26.5
Grassland			
Cropland	30	75	57
Wetland	6	1	1
Plantations	8	1.4	3.8
Dense bush clumps with indigenous forest patch	4	0	1
Dam sites	3	6	3
Others	4	4.6	7.7

(*Chlorocebus pygerythrus*), samango monkey (*Cercopithecus albogularis*), chacma baboons (*Papio ursinus*), scrub hare (*Lepus saxatilis*), cape porcupine (*Hystrix africaeaustralis*), serval (*Leptailurus serval*), caracal (*Felis caracal*), black-backed jackal (*Canis mesomelas*), large grey mongoose (*Herpestes ichneumon*), white-tailed mongoose (*Ichneumia albicauda*), water mongoose (*Atilax paludinosus*), large-spotted genet (*Genetta tigrina*), African wild cat (*Felis lybica*) and feral cat (*F. catus*) (Rowe-Rowe 1992, 1994). We selected three sampling areas according to varied intensity of land use, and land-cover characteristics (Geoterralmage 2010, Fig. 1 and Table 1). The main land uses in this region are dairy production using indigenous grassland pasture, seed potatoes *Solanum tuberosum* and maize *Zea mays*. The minimum convex polygon size of the camera survey areas was 43.2 km<sup>2</sup> for A and 35 km<sup>2</sup> for both B and C.

To document occupancy and relative abundance of mammals in the farmland, we conducted camera trapping survey between October 2012 and January 2013 using a systematic grid 2 km<sup>2</sup> covering all three different sites varied in land use patterns at 44 locations. We did not have large number of traps (15 traps) whereas we had to choose appropriate grid size 2 km<sup>2</sup> that represented most of the mammal species presence in the study area based on other published papers and our field knowledge (Ramesh et al. 2013). In total, we had 43.2 km<sup>2</sup> grids across the study areas and camera trapping survey was done on rotational basis to sample a larger area. Each grid had a minimum of one camera trap site with mean inter-trap distance of 1.7 km. Each camera was operated for 30 days amounting to a total effort of 1320 trap nights. Trap-stations were distributed covering three sampling areas. Photographs can provide large set of data on species distribution and abundance of mammals and this can be collected using camera traps (Kinnaird and O'Brien 2012; Pettorelli et al. 2010; Ramesh et al. 2012; Ramesh et al. 2013; Rowcliffe & Carbone 2008; Tobler et al. 2009). These surveys used fixed cameras (Camera Ltl Acorn® 6210MC, Shenzhen Ltl Acorn Electronics Co. Ltd., China), triggered by passive infrared sensors to “capture” digital photographs of passing animals and for more detail see Ramesh and Downs (2013). Cameras were placed along animal trails at approximately 20 cm above the ground to capture all encountering mammalian species and were left to operate for 24 h a day. We classified all animal photographs to species level and grouped photographic sequences into independent photographic events, where we considered all the photos taken per 5 min as one event. As estimation of abundance or density is difficult for many species, measure of relative abundance index (RAI) is a basic substitute for abundance. We used the number of independent photographic events per 100 trap days as RAI, and presence/absence of species in camera trapping sites during sampling session as occupancy of mammals. We generated mammalian species detection history (1100100) for each camera location consisting of values ‘1’ indicating species detection during the sampling occasion and ‘0’ indicating non-detection (Otis et al. 1978). Site occupancy is defined as the proportion of area or sites occupied



**Fig. 1.** Map of the three study sites with camera trap stations on farmland, Drakensberg Midlands, KwaZulu-Natal, South Africa. (A) Less farmed and more natural habitat; (B) intensively farmed habitat; and (C) semi-farmed habitat.

by a species (MacKenzie et al. 2006). Naive occupancy is the estimate of occupancy ignoring detection, i.e., provided the site where the species was detected at least once (MacKenzie et al. 2006). The detection probability is the probability of detecting the species that can be achieved by repeated surveys of the sites and that enables unbiased estimation of site occupancy (MacKenzie et al. 2006). We did not estimate occupancy and detection probabilities for duiker that had naive occupancy 1.0 (Hines, personal communication) and other species with very low captures.

We used ArcGIS 9.3.1 (ESRI, Redlands, CA, USA) to extract area of available habitats such as crop land, wetland, patch of dense forest, bushland and plantation available at each camera site within 1 km buffer from the latest classified land cover map 2008 of KwaZulu-Natal (Geoterralmage 2010). Using the program ArcGIS 9.3.1 we reclassified the original land-cover types into six categories which are representative of the study site in the Midlands: cropland, wetland, grassland, dense forest, bushland and plantation. The camera traps were placed in proportion to habitat availability. Independent photographic capture rate per 100 trap nights of livestock (cattle, sheep and horse), and human activities (human and vehicle movements) were estimated from each camera site. The pesticide usage on rodent population especially with bushveld gerbil *Gerbilliscus leucogaster* which form large colonies, appeared to have a negative impact on many carnivore species (personal communication). Therefore we have noted pesticide use within 500 m around each camera site as presence (1) and absence (0) scale. This information was gathered from either farmland owners or their staff depending on the experienced persons available.

Site occupancy is known to provide an unbiased estimate of species status and cost-effective for large-scale monitoring of

multiple species (Sarmiento et al. 2011; Kinnaird and O'Brien 2012). The camera trapping period was restricted to 30 days to minimize the likelihood of changes in occupancy. The 30-day datasets were classified into 10 sampling periods of 3 days each to increase detection probability for each sampling period without violating population closure assumptions. We used the single-season occupancy model (MacKenzie et al. 2006) to estimate probability of a given site occupied by a species  $\psi$  and detection probability  $p$ . The detection histories of target species were constructed under a standard "X-matrix format" for each camera-trap location for 10 sampling occasions (Otis et al. 1978). We used the program PRESENCE 5.5 (Hines 2006) for all analyses of species distribution with covariates. We considered continuous site covariates such as cropland, wetland, patches of dense forest, bushland, natural grassland and plantation as covariates of occupancy at each site. We standardized all continuous site covariates to z-scores prior to analysis which allows model coefficients to be interpreted as the change in the log-odds ratio of occupancy relative to a 1-standard deviation change in a covariate from its mean (Cooch & White 2005). We also included covariates measured at camera points: z-scores of RAI for livestock, and human. Presence/absence pesticide usage at camera points was a categorical variable. Correlations among independent variables were tested to avoid problems with multicollinearity (Graham 2003). We included independent variables in the models when the explanatory factor was  $p \leq 0.05$ . A global model was produced that contained all potential covariates for occupancy and allowed detection probability ( $p$ ) to vary by all covariates. We used two-step procedure wherein we initially modelled  $p$  and then modelled  $\psi$ . The potential covariates for occupancy were then allowed to vary, individually or in combination, while



detection was either maintained in the global model or remained constant, i.e.,  $\psi_{\text{covariate}}p_{\text{covariate}}$ , or  $\psi_{\text{covariate}}p$ . The simplest model was also considered where both occupancy and detection probability remained constant,  $\psi \cdot p$ . We assessed model fit by estimating the mean dispersion parameter  $\hat{c}$  for the model using 10 000 parametric bootstraps as recommended by MacKenzie and Bailey (2004). We assumed that models with  $\hat{c}$  values of  $\sim 1$  were adequate descriptors of the data whereas models with  $\hat{c} > 1$  suggested that there was more variation in the observed data than expected by the model (Burnham & Anderson 2002). We prioritized model selection for each species by minimum  $\Delta\text{AIC} \leq 2$  and deleted models with  $w_i \leq 0.05$  (Burnham & Anderson 2002). Model averaging was used to estimate  $\psi$ ,  $p$ , and covariate coefficients (Burnham & Anderson 2002) when multiple models provided adequate descriptions of the data to compare their relative importance for each species. We then compared results for covariate types across analyses on site occupancy and likelihood detection of mammals.

We evaluated independent covariate effects on relative abundance of mammals with the RAI of independent photographs (O'Brien et al. 2003). We normalized the RAI values within species on the basis of z-scores. The significant effect of independent covariates on each species was analysed with General Linear Models (GLM) with RAI of mammalian species as the dependent variable and land use variables as independent covariates. The test was computed with a significance level of 0.05 using SPSS 16.0/PC+ software (SPSS 2007).

### Results

Thirty days of camera trapping at 44 sites,  $n = 1320$  trap-nights yielded 3575 independent photo captures of 25 species of wild mammals, livestock and human (Appendix A). We did not conduct occupancy models on species with a naive occupancy of 1.0 (e.g., duiker). Of the 26 species captured, we focused on site occupancy and abundance analyses of 10 species for which we had sufficient data (naive occupancy  $\geq 0.20$ ). These were serval  $n = 286$ , jackal  $n = 609$ , water mongoose  $n = 65$ , white-tailed mongoose  $n = 29$ , large grey mongoose  $n = 146$ , common grey duiker  $n = 528$  (only relative abundance analysis due to naive occupancy 1.0), bush buck  $n = 104$ , reed buck  $n = 337$ , bush pig  $n = 110$  and porcupine  $n = 536$ . Models for species with low detections failed to converge, and hence we did not consider them in our analyses.

The number of variables influencing patterns of occupancy and detection probability in well-supported models (model weight  $w_i > 0.11$ ) ranged from 2 to 6 (Table 1). We determined top models for each species and their average untransformed parameter estimates of site occupancy  $\psi$  and detection probability  $p$  with results listed in Tables 2 and 3, respectively. The estimation of occupancy and detection probability greatly reduced the total number of candidate models for comparison. Naive occupancy was highest for porcupine 0.86, followed by serval 0.84, jackal 0.79, reed buck 0.72, large grey mongoose 0.65, water mongoose 0.50, white-tailed mongoose 0.40, bush pig 0.40 and bush buck 0.38. Estimates of site occupancy  $\psi$  with standard errors varied from  $0.43 \pm 0.08$  to  $0.88 \pm 0.07$  across all species and models. No single model emerged as the top ranking model except for bush pig, so the averaged model occupancy was chosen as the final estimate, which corresponds to a small difference from the naive site occupancy of mammals. Porcupine, jackal, serval and reed buck were the most commonly captured mammals with high estimates for both site occupancy  $\geq 0.73$  and detection  $\geq 0.36$  (Fig. 2). Bush buck and white-tailed mongoose had lower detection probability than other species. The species with low detection requires substantial effort to model site occupancy. Caution should be taken while

**Table 2**  
Top logistic models for predicting the occupancy and detection probability of nine mammal species in the study sites.

Species	Model	AIC	$\Delta\text{AIC}$	AIC wgt	Model likelihood	No. Par.	–2LL	$\psi \pm \text{SE}$	$p \pm \text{SE}$
Serval	$\psi/\text{CROP} + \text{H}, p/\text{WETL} + \text{H} + \text{LVST}$	511.33	0.00	0.549	1.00	7	497.33	$0.88 \pm 0.07$	$0.36 \pm 0.04$
Jackal	$\psi/\text{CROP} + \text{H}, p/\text{WETL} + \text{H}$	512.21	0.88	0.354	0.64	6	500.21	$0.87 \pm 0.07$	$0.37 \pm 0.03$
	$\psi/\text{WETL}, p/\text{H} + \text{PEST} + \text{LVST}$	475.30	0.00	0.217	1.00	6	463.30	$0.80 \pm 0.07$	$0.47 \pm 0.04$
	$\psi/\text{WETL}, p/\text{H} + \text{PEST} + \text{LVST} + \text{PLANT}$	476.00	0.70	0.153	0.70	7	462.00	$0.80 \pm 0.07$	$0.47 \pm 0.05$
	$\psi/\text{WETL}, p/\text{H} + \text{PEST} + \text{LVST} + \text{CROP}$	476.62	1.32	0.112	0.52	7	462.62	$0.80 \pm 0.07$	$0.47 \pm 0.05$
Large Grey Mongoose	$\psi/\text{PLANT} + \text{CROP}, p/\text{H} + \text{LVST} + \text{PLANT} + \text{F}$	397.30	0.00	0.475	1.00	8	381.30	$0.73 \pm 0.11$	$0.27 \pm 0.05$
	$\psi/\text{PLANT} + \text{CROP}, p/\text{H} + \text{LVST} + \text{PLANT}$	399.20	1.90	0.184	0.39	7	385.20	$0.68 \pm 0.11$	$0.30 \pm 0.04$
Water Mongoose	$\psi/\text{F} + \text{PLANT} + \text{WETL}, p/\text{H} + \text{CROP} + \text{PEST}$	229.57	0.00	0.542	1.00	8	213.57	$0.57 \pm 0.10$	$0.23 \pm 0.04$
	$\psi/\text{F} + \text{PLANT}, p/\text{H} + \text{CROP} + \text{PEST}$	230.97	1.40	0.269	0.50	7	216.97	$0.55 \pm 0.11$	$0.21 \pm 0.03$
White-tailed Mongoose	$\psi/\text{CROP}, p/\text{LVST}$	198.18	0.00	0.480	1.00	4	190.18	$0.66 \pm 0.07$	$0.10 \pm 0.02$
	$\psi/\text{CROP}, p$	198.94	0.76	0.329	0.68	3	192.94	$0.65 \pm 0.08$	$0.10 \pm 0.02$
Bush Buck	$\psi/\text{F} + \text{PLANT} + \text{WETL}, p/\text{H} + \text{CROP} + \text{PEST}$	229.57	0.00	0.542	1.00	8	213.57	$0.54 \pm 0.13$	$0.16 \pm 0.04$
	$\psi/\text{F} + \text{PLANT}, p/\text{H} + \text{CROP} + \text{PEST}$	230.97	1.40	0.269	0.50	7	216.97	$0.56 \pm 0.14$	$0.16 \pm 0.04$
Bush Pig	$\psi/\text{F} + \text{WETL} + \text{CROP} + \text{PLANT} + \text{LVST} + \text{H}, p/\text{PLANT} + \text{CROP}$	244.83	0.00	0.829	1.00	10	224.83	$0.43 \pm 0.08$	$0.30 \pm 0.05$
Reed Buck	$\psi/\text{F} + \text{H}, p/\text{WETL} + \text{CROP} + \text{PLANT}$	483.48	0.00	0.334	1.00	7	469.48	$0.73 \pm 0.09$	$0.42 \pm 0.05$
	$\psi/\text{F} + \text{H} + \text{WETL}, p/\text{WETL} + \text{CROP} + \text{PLANT}$	483.81	0.33	0.283	0.85	8	467.81	$0.73 \pm 0.10$	$0.42 \pm 0.05$
Porcupine	$\psi/\text{LVST}, p/\text{CROP} + \text{WETL}$	534.65	0.00	0.503	1.00	5	524.65	$0.88 \pm 0.06$	$0.47 \pm 0.04$
	$\psi/\text{H}, p/\text{CROP} + \text{WETL}$	536.49	1.84	0.200	0.40	5	526.49	$0.87 \pm 0.07$	$0.47 \pm 0.04$

Abbreviations: We list all models with a delta Akaike Information Criterion  $\Delta\text{AIC} < 2.00$ . Twice the likelihood –2LL, number of parameters No. par., estimated occupancy  $\psi$ , estimated detection probability  $p$  is presented for each model, Area of cropland availability CROP, Area of wetland availability WETL, Area of plantation availability PLANT, Area of forest availability F, Relative abundance of human H and livestock LVST, and presence or absence of pesticide use on rodent within 500 m of camera each location PEST.

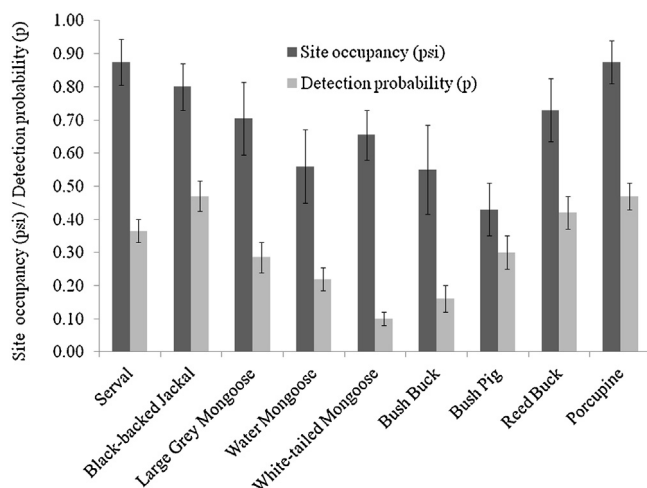
**Table 3**

Untransformed parameter estimates for explanatory variables from the best occupancy and detection probability model for nine species of mammals in the study sites.

Species	Site detection probability			Site occupancy		
	Covariates	Estimate	Standard error	Covariates	Estimate	Standard error
Serval	Intercept	−0.57	0.12	Intercept	4.68	2.44
	WETL	0.45	0.11	CROP	−2.05	1.20
	H	0.32	0.09	H	4.54	3.46
	LVST	0.18	0.11			
Jackal	Intercept	0.34	0.17	Intercept	2.10	0.82
	H	0.79	0.16	WETL	1.92	1.36
	PEST	−0.72	0.25			
	LVST	0.37	0.14			
	CROP	−0.09	0.11			
Large Grey Mongoose	Intercept	−1.18	0.28	Intercept	1.12	0.47
	H	0.53	0.15	PLANT	1.18	0.84
	LVST	−0.35	0.20	CROP	0.76	0.48
	PLANT	0.32	0.14			
	F	−2.45	1.60			
Water Mongoose	Intercept	−1.32	0.19	Intercept	1.50	0.77
	H	0.33	0.15	PEST	−2.18	0.89
	F	−0.40	0.26			
White-tailed Mongoose	Intercept	−2.19	0.21	Intercept	3.11	2.83
	LVST	−0.42	0.30	CROP	6.92	5.12
Bush Buck	Intercept	−1.17	0.30	Intercept	27.65	3.73
	H	0.88	0.18	F	102.19	14.00
	CROP	−0.59	0.22	PLANT	1.94	1.43
	PEST	−1.98	0.56	WETL	1.31	1.05
Bush Pig	Intercept	−0.91	0.18	Intercept	9.93	7.16
	PLANT	0.51	0.13	F	47.25	30.38
	CROP	0.68	0.19	WETL	3.02	1.55
				CROP	3.06	1.81
				PLANT	10.11	4.64
				LVST	1.86	0.96
				H	−7.87	3.28
Reed Buck	Intercept	−0.33	0.12	Intercept	0.82	0.76
	WETL	0.27	0.12	F	−4.37	2.95
	CROP	0.16	0.14	H	1.87	1.07
	PLANT	0.16	0.11	WETL	0.60	0.52
Porcupine	Intercept	−0.10	0.11	Intercept	2.06	0.52
	CROP	−0.41	0.11	LVST	−0.62	0.38
	WETL	0.44	0.13	H	−0.38	0.37

inferring the results as our survey focused on multiple species simultaneously.

Cropland use and wetland availability was an important feature for most mammals. Occupancy of serval was negatively influenced



**Fig. 2.** Detection probability  $p$  and site occupancy  $w$  estimates for nine mammal species across the three study sites.

by high cropland use while it had a positive influence on other species such as large grey mongoose, water mongoose and bush pig. The detection probability of jackal, bush buck and porcupine were negatively influenced by cropland use. The availability of wetland was positively associated with occupancy of jackal, bush buck, reed buck and bush pig. Wetland had a positive effect on the detection probability of serval, reed buck and bush pig. Wetland was the only variable positively supporting both occupancy and detection probability of most mammals. Relative human abundance, and livestock activities were the second most common factors selected by models. Occupancy of serval and reed buck was positively influenced by relative human abundance while it negatively influenced occupancy of porcupine and bush pig. Effects of relative human abundance during sampling on species occupancy were highly variable. Relative human abundance did not have negative influence on the detection of many mammal species. Livestock-related activity was positively associated with occupancy of bush pig and negatively with porcupine while it showed positivity with detection of serval and jackal, and negativity with large grey mongoose and white-tailed mongoose. Occupancy of carnivores was least associated with livestock-related activity, as most carnivores are nocturnal. Overall pesticide usage had strong negative effects on several mammals' detection probability, and occupancy of water mongoose. Occupancy of bush buck and bush pig showed a positive relationship with forest while reed buck had a negative

relationship. Detection probabilities of large grey mongoose and water mongoose decreased with presence of forest. Proximity to plantation was positively associated with occupancy of large grey mongoose, bush buck and bush pig, and detection probability with five other mammal species.

We used RAls as surrogates for species-specific relative abundance to model the independent effects of covariates as RAl was found to vary greatly among species at different sites. Among all mammals, wetland influenced the relative abundance of serval ( $p=0.02$ ) (Table 4). Although, pesticide usage on rodents affected abundance of several mammalian species, its effect varied significantly on serval and water mongoose ( $p<0.05$ ). In addition, relative livestock and human abundance positively influenced the relative abundance of serval and jackal ( $p<0.05$ ; Table 4) while these variables negatively affected relative abundance of many other mammals. Plantation had significant positive effect on the relative abundance of jackal, bush buck, bush pig, reed buck and large grey mongoose ( $p<0.05$ ). Cropland use and forest did not influence relative abundance of mammals. The number of independent photographs for all mammal species captured in the camera traps is given in Appendix A.

## Discussion

Our assessment of 10 different mammalian species provided novel insights to understand the conservation value of farmland habitats. Response to disturbance varies among mammals often in relation to body size and home range size and with the level of disturbance (Estrada et al. 1994; Martinoli et al. 2006). However, researchers have documented a capacity for tolerance in various mammals to disturbances (Jansen et al. 2007; Kolowski and Alonso 2010; Lawler et al. 2004). The biology of the species might determine ecological flexibility of the species in an ecosystem as well (Cardillo et al. 2004). We compared the occupancy patterns and relative abundance of mammals in various land use forms. In view of our predictions, some species were highly sensitive to reduction of natural habitat because of their dependence on native habitats while others showed partial or total tolerance to human-modified habitats. Such exposure to habitat loss is the source of decline of mammal species. Our study provided a preventive approach to species extinction by identifying important predictors influencing mammal relative abundance. However, the small number of camera traps and the short period of investigation should be considered further as this could affect the detection rate of mammals.

Intensification of agricultural practices for cropland or permanent pasture were found to reduce the extent and quality of natural habitat on agricultural land and such intensification was reported to affect prey availability of carnivores forcing them to a highly imbalanced diet (Green et al. 2005; Remonti et al. 2011). Consequently, that reduces shelter and food for carnivores. In relation to this, we found that the occupancy of serval showed negative association with availability of cropland, and mongooses showed positivity with cropland which suggests that the heterogeneity in niche dimension with regards to local land uses may promote biodiversity by allowing existence of complimentary sets of species (Schuette et al. 2013). Detection probability of jackal showed negativity towards croplands possibly due to greater persecution of the species in croplands “e.g., heavily persecuted species like spotted hyena *Crocuta crocuta*” become more secretive or nocturnal in highly modified landscapes (Boydston et al. 2003). Such behavioural changes in a dominant species like jackal may initiate ‘behavioural release’ in subordinate species. Alternatively, variation in land use might sustain some wetland species that completely depend on wetland habitat in the mosaic of cropland. Herbivores like reed buck were positively detected in the cropland.

Though bush pigs favour natural habitats like forest and dense cover, they are attracted to human-induced modified habitats due to availability of maize and vegetables at night (pers. obs.). This could be a reason for the positive response of wild pig occupancy in croplands. This habitat is a part of a mosaic landscape, and the presence of species in a habitat can be a function of not only that particular habitat but also the type of neighbouring habitat.

Wetland habitats have higher density of small mammals than other habitats which is considerably important for carnivores in a mosaic landscape (Bowland & Perrin 1993). Serval occupancy was not influenced by wetland significantly while they were to be detected well near wetland. However the RAl of serval was significantly influenced by wetland. Occupancy of jackal was mainly supported by wetland. Since both species are wide ranging and  $\geq 50\%$  of their diet comprises of small mammals (Bowland 1990; Rowe-Rowe 1992), this suggests their likely presence near wetlands. In addition, jackals often kill livestock, reed buck, and duiker and wetlands provide good refuge for hunting. Interestingly none of the species were negatively influenced by availability of wetland, and showed significant positive association with occupancy of herbivores and detection of porcupine. Both occupancy and detection of reed buck increased with availability of wetland mainly due to their dependence on year round nutritious food sources and good cover. This shows the significance of wetlands in terms of conservation, management, and forage availability for a diverse range of species within a mosaic of farmland.

Occupancy of bush buck and bush pig were mainly related to availability of forested patches and plantations. This supported bush buck's wider habitat preference towards dense forested vegetation and feeding mostly from the browsable vegetation (Rowe-Rowe 1994). Bush pig probably favoured these habitats due to the presence of wet forest soil which is easier to dig to look for underground roots (Ghiglieri et al. 1982; Nummelin 1990; Rowe-Rowe 1994). Reed buck showed a negative relationship with forest due to their grazing nature, water dependency, and preference towards native habitat such as marsh wetlands with tall reed beds (Rowe-Rowe 1994). Large grey mongoose occupancy was favoured by proximity to plantation due to preference towards dense vegetation cover in the matrix of farmlands and moist grassland (Maddock 1988; Maddock & Perrin 1993). Proximity to plantation showed strong positive effects on the abundance of jackal, bush buck, bush pig, reed buck and large grey mongoose. Plantation was associated with the detection probability of many mammals since it provides a refuge in the absence of forest patches in the open mosaic of farmlands. These responses of species to forest depend on species' specific habitat requirements, and forest loss often leads to decline in the distribution of forest specialists (Erb et al. 2012). Studies have indicated the importance of quantity and quality of available forest to species occurrence (Ceballos & Brown 1995; White et al. 1997) and our results supported these findings.

Wetland specialists like serval and reed buck showed a positive association towards relative human abundance due to their dependence on available wetlands (Bowland & Perrin 1993; Rowe-Rowe 1992), and availability of most of the wetlands are amidst cropland and pastures where human activities are predominant. In addition human and livestock-related activities had a significant positive impact on the relative abundance of serval and jackal positively while it negatively affected the relative abundance of many other mammals. This shows that some species are dependent and tolerant to human modified habitats. However relative abundance of humans negatively affected the occupancy of bush pig and porcupine which could be related to persecution of these species.

Increased livestock-related activities decreased occupancy of some species while it increased for others (Kinnaird and O'Brien 2012). Species whose distribution benefited from livestock were uncommon. Bush pig occupancy was positively supported by

**Table 4**

Generalised linear models discriminating independent variable effect on relative abundance of 10 species of mammals in the study sites.

Dependent Variable	Model	Parameter estimate	Standard error	t-Value	p-Value
Serval	Intercept	0.24	0.17	1.40	0.17
	PLANT	0.16	0.13	1.21	0.23
	WETL	0.28	0.12	2.32	0.03
	CROP	-0.03	0.14	-0.24	0.81
	F	0.03	0.13	0.22	0.82
	LVST	0.46	0.12	3.74	0.00
	H	0.37	0.14	2.74	0.01
	PEST	-0.45	0.25	-1.83	0.04
Jackal	Intercept	0.19	0.16	1.16	0.26
	PLANT	0.45	0.13	3.52	0.00
	WETL	0.19	0.11	1.68	0.10
	CROP	0.00	0.13	0.01	0.99
	F	0.18	0.12	1.50	0.14
	LVST	0.29	0.12	2.53	0.02
	H	0.37	0.13	2.84	0.01
	PEST	-0.30	0.23	-1.28	0.21
Large Grey Mongoose	Intercept	-0.21	0.22	-0.98	0.34
	PLANT	0.46	0.17	2.69	0.01
	WETL	-0.17	0.16	-1.12	0.27
	CROP	0.19	0.18	1.05	0.30
	F	-0.07	0.16	-0.41	0.69
	LVST	-0.15	0.16	-0.97	0.34
	H	-0.01	0.17	-0.08	0.94
	PEST	0.31	0.32	0.98	0.34
White-tailed Mongoose	Intercept	-0.10	0.24	-0.43	0.67
	PLANT	0.07	0.19	0.38	0.71
	WETL	-0.20	0.17	-1.21	0.24
	CROP	0.05	0.19	0.25	0.80
	F	-0.04	0.18	-0.20	0.85
	LVST	0.29	0.17	1.70	0.10
	H	-0.05	0.19	-0.27	0.79
	PEST	0.21	0.35	0.60	0.55
Water Mongoose	Intercept	0.33	0.23	1.45	0.16
	PLANT	0.11	0.18	0.62	0.54
	WETL	-0.16	0.16	-0.97	0.34
	CROP	-0.12	0.18	-0.66	0.52
	F	-0.21	0.17	-1.23	0.23
	LVST	0.16	0.16	0.97	0.34
	H	0.10	0.18	0.56	0.58
	PEST	-0.69	0.33	-2.10	0.04
Common Grey Duiker	Intercept	-0.43	0.23	-1.90	0.07
	PLANT	0.22	0.18	1.25	0.22
	WETL	0.23	0.16	1.46	0.15
	CROP	0.18	0.18	0.97	0.34
	F	0.02	0.17	0.14	0.89
	LVST	-0.03	0.16	-0.19	0.85
	H	-0.16	0.18	-0.90	0.38
	PEST	0.83	0.33	2.55	0.15
Porcupine	Intercept	0.13	0.25	0.51	0.61
	PLANT	-0.10	0.19	-0.54	0.60
	WETL	0.13	0.18	0.71	0.48
	CROP	-0.20	0.20	-1.01	0.32
	F	-0.05	0.19	-0.26	0.80
	LVST	-0.17	0.18	-0.95	0.35
	H	0.12	0.20	0.59	0.56
	PEST	-0.19	0.36	-0.52	0.61
Reed Buck	Intercept	-0.04	0.22	-0.17	0.86
	PLANT	0.48	0.17	2.73	0.01
	WETL	0.06	0.16	0.37	0.71
	CROP	0.05	0.18	0.25	0.80
	F	-0.06	0.17	-0.37	0.71
	LVST	0.02	0.16	0.14	0.89
	H	0.08	0.18	0.47	0.64
	PEST	0.02	0.32	0.07	0.95
Bush Buck	Intercept	0.11	0.18	0.61	0.55
	PLANT	0.55	0.14	3.92	0.00
	WETL	-0.04	0.13	-0.33	0.75
	CROP	-0.11	0.15	-0.77	0.45
	F	0.10	0.14	0.76	0.45
	LVST	-0.08	0.13	-0.59	0.56
	H	0.16	0.14	1.13	0.27
	PEST	-0.27	0.26	-1.03	0.31
Bush Pig	Intercept	-0.09	0.20	-0.43	0.67
	PLANT	0.71	0.16	4.53	0.00
	WETL	0.17	0.14	1.20	0.24
	CROP	0.31	0.16	1.96	0.06
	F	0.15	0.15	0.98	0.34
	LVST	0.03	0.14	0.24	0.82
	H	-0.19	0.16	-1.19	0.24
	PEST	0.12	0.29	0.43	0.67



relative livestock abundance, and porcupine occupancy and detection probability of mongooses was negatively influenced by relative livestock abundance. Although small and medium-sized carnivores are still common in farmlands, studies have shown that small carnivores are locally declining due to grazing-induced changes in the landscape structure (Blaum et al. 2007, 2009). Species occupancy was less sensitive to livestock-related activity than other variables. Overall, the effect of livestock-related activities may result in displacement and disappearance of large grazers and browsers (Kinnaid and O'Brien 2012; Parmenter et al. 1995). Though farmland owners tolerate predators, they have negative attitudes toward jackals. Jackals are often identified as problem animals and are the most likely carnivores to be killed by humans for feeding over livestock in farmland ecosystems. The local perception of jackal as common livestock predators and frequent raiders of subsistence farms, supported our models that showed its increased detection with livestock abundance, as they are capable of attacking livestock calves, sheep and goats. Our results show that it is possible that areas used by people and livestock can still support some species that are tolerant to human activities.

The use of pesticides on rodent species is problematic where conservation issues are concerned. Since water mongooses are closely associated with water sources with a 50% diet comprising of aquatic prey, they become more vulnerable to water pollution due to pesticide load (Rowe-Rowe 1992). Hence this species occupancy showed a strong negative response to pesticide use than other species. The population of predators in the farmland can decline largely as a consequence of small mammal poisoning. In addition, pesticide use affected relative abundance of several mammalian species meanwhile its effect was strong on serval and water mongoose. Small mammals are one of the most important prey for predators. Pesticide use on rodents can cause accidental secondary poisoning if poisoned rodents are consumed. Overall pesticide use on rodent population in the study areas had a negative effect on several mammals' especially the relative abundance of serval and detection of jackal. This indicates that management actions and prioritisation of habitat conservation should minimize chances of poisoning on rodents due to its negative consequences on population dynamics of mammalian carnivores and other raptors.

### Conservation implications

Our study provided a quantitative approach for planned decision making in multi-species conservation by accounting several land use variables. Multi-species modelling inform land managers that models predicted the consequences of changes in land use for several mammalian species. Protection of suitable habitats such as wetlands, natural grassland and forest patches must be encouraged through continued reforestation and restoration as this would be extremely beneficial to a diverse range of mammalian species in formulating new and informed land use policies. The negative consequences of pesticide use on small mammal and carnivore populations should be taken into consideration through eco-awareness campaigns among farmland owners. Many conservation biologists argue that the application of wildlife-friendly farming methods would reduce the impact of land use intensity on biodiversity (Green et al. 2005). The retention of patches of natural habitat in a mosaic of farmland habitats in a way could reduce the negative effects on wildlife. The positive association between relative human abundance and occupancy of some mammalian species suggests biodiversity could be maintained by retaining a mosaic of natural habitats within the managed landscapes. Conservation agencies should increase the level of community participation in establishment of community wildlife-conservation areas and provide incentives and compensation for wildlife damage on

private properties. Finally, the conservation of biodiversity in sub-tropical natural habitat/farmland mosaics can only be successful through integrated policy and management that consider both natural and farmland ecosystems from a landscape point of view. Therefore, strategies for biodiversity conservation and management should not only target PAs but also managed land which can also host significant wildlife species.

Conservation science can help in political decision making and framing policies regarding land-use approaches by providing information on biodiversity value (Barlow et al. 2007). We caution decision makers in drawing firm conclusions from studies that focus on limited taxa with certain land use type as the complex role of several mammal species is involved. These observations could provide a framework for continued, successful wildlife conservation outside PAs and serve as a model for human-modified habitats across the world.

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### Appendix A. Independent photographs of mammals captured in camera traps in the study sites

Mammals	Scientific name	Independent photos
African Wild Cat	<i>Felis lybica</i>	5
Aardvark	<i>Orycteropus afer</i>	6
Chacma Baboon	<i>Papio ursinus</i>	43
Black-backed Jackal	<i>Canis mesomelas</i>	609
Bush Buck	<i>Tragelaphus scriptus</i>	104
Bush Pig	<i>Potamochoerus larvatus</i>	110
Cape Clawless Otter	<i>Aonyx capensis</i>	6
Scrub hare	<i>Lepus saxatilis</i>	33
Caracal	<i>Felis caracal</i>	7
Common Grey Duiker	<i>Sylvicapra grimmia</i>	528
Feral Cat	<i>Felis catus</i>	24
Human	<i>Homo sapiens</i>	403
Rock Hyrax	<i>Procavia capensis</i>	1
Large Spotted Genet	<i>Genetta tigrina</i>	22
Large Grey Mongoose	<i>Herpestes ichneumon</i>	146
Livestock	–	280
Striped Polecat	<i>Ictonyx striatus</i>	2
Cape Porcupine	<i>Hystrix africaeaustralis</i>	536
Common Reed Buck	<i>Redunca arundinum</i>	337
Serval	<i>Leptailurus serval</i>	286
Slender Mongoose	<i>Galerella sanguinea</i>	1
Small Spotted Cat	<i>Felis nigripes</i>	1
Samango Monkey	<i>Cercopithecus albogularis</i>	1
Spot-necked Otter	<i>Lutra maculicollis</i>	1
Vervet Monkey	<i>Chlorocebus pygerythrus</i>	13
Water Mongoose	<i>Atilax paludinosus</i>	65
White-tailed Mongoose	<i>Ichneumia albicauda</i>	29

### References

- Barlow, J., Gardner, T. A., Araujo, I. S., Ávila-Pires, T. C., Bonaldo, A. B., Costa, J. E., et al. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 18555–18560.
- Blaum, N., Rossmanith, E., Schwager, M., & Jeltsch, F. (2007). Responses of mammalian carnivores to land use in arid savanna rangelands. *Basic and Applied Ecology*, 8, 552–564.



- Blaum, N., Tietjen, B., & Rossmanith, E. (2009). Impact of livestock husbandry on small- and medium-sized carnivores in Kalahari Savannah rangelands. *Journal of Wildlife Management*, 73, 60–67.
- Bowland, J. M. (1990). *Diet, home range and movement pattern of serval on farmland in Natal* (M.Sc. thesis). Pietermaritzburg: University of Natal.
- Bowland, J. M., & Perrin, M. R. (1993). Wetlands as reservoirs of small mammal populations in the Natal Drakensberg. *South African Journal of Wildlife Research*, 23, 39–43.
- Boydston, E. E., Kapheim, K. M., Szykman, M., & Holekamp, K. E. (2003). Individual variation in space use by female spotted hyenas. *Journal of Mammalogy*, 84, 1006–1018.
- Briggs, D. I., & Courtney, F. M. (1989). *Agriculture and environment*. Harlow: Longman.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (second ed.). New York: Springer-Verlag.
- Carbone, C., et al. (2001). The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, 4, 75–79.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J., & Mace, G. M. (2004). Human population density and extinction risk in the World's carnivores. *PLoS Biology*, 2, 909–914.
- Ceballos, G., & Brown, J. H. (1995). Global patterns of mammalian diversity, endemism, and endangerment. *Conservation Biology*, 9, 559–568.
- Ceballos, G., & Ehrlich, P. (2006). Global mammal distribution, biodiversity hotspots and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 19374–19379.
- Cingolani, A. M., Noy-Meir, I., & Diaz, S. (2005). Grazing effects on rangeland diversity, a synthesis of contemporary models. *Ecological Application*, 15, 757–773.
- Cooch, E., & White, G. (2005). *Program MARK: A gentle introduction*. <http://www.phidot.org/software/mark/docs/book>
- Crooks, K. R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology*, 16, 488–502.
- Erb, P. L., McShea, W. J., & Guralnick, R. P. (2012). Anthropogenic influences on macro-level mammal occupancy in the Appalachian Trail corridor. *PLoS ONE*, 7, e42574.
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., et al. (2011). Trophic downgrading of planet earth. *Science*, 333, 301–306.
- Estrada, A., Coates-Estrada, R., & Merritt, D., Jr. (1994). Non-flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. *Ecography*, 17, 229–241.
- Fitzherbert, E. B., Struebig, M., Morel, A., Danielsen, F., Bruhl, C., Donald, P., et al. (2008). How will oil palm expansion affect biodiversity? *Trends in Ecology and Evolution*, 23, 538–545.
- Gall, G. A. E., & Orians, G. H. (1992). Agriculture and biological conservation. In G. A. E. Gall, & S. Mary (Eds.), *Integrating conservation biology and agricultural production. Agriculture Ecosystem and Environment*, 42, 1–8.
- Geoterrimage. (2010). *2008 KZN province land-cover mapping (from SPOT5 Satellite imagery circa 2008)*. South Africa: Prepared for Ezemvelo KZN Wildlife (Biodiversity Research).
- Ghiglieri, M. P., Butynski, T. M., Struhsaker, T. T., Leland, L., Wallis, S. J., & Waser, P. (1982). Bush pig (*Potamochoerus porcus*) polychromatism and ecology in Kibale Forest, Uganda. *African Journal of Ecology*, 20, 231–236.
- Gilpin, M., Gall, G. A. E., & Woodruff, D. S. (1992). Ecological dynamics and agricultural landscapes. Integrating conservation biology and agricultural production. *Agriculture Ecosystem and Environment*, 42, 27–52.
- Graham, M. H. (2003). Confronting multicollinearity in ecological multiple regression. *Ecology*, 84, 2809–2815.
- Green, R. E., Cornell, S. J., Scharlemann, J. P. W., & Balmford, A. (2005). Farming and the fate of wild nature. *Science*, 307, 550.
- Haines-Young, R. (2009). Land use and biodiversity relationships. *Land Use Policy*, 26, S178–S186.
- Hines, J. E. (2006). *PRESENCE – Software to estimate patch occupancy and related parameters*. USGS-PWRC. <http://www.mbr-pwrc.usgs.gov/software/presence.html>
- Homewood, K., & Rodgers, W. A. (1991). *Masailand ecology: Pastoralists, development and wildlife conservation in Ngorongoro conservation area, Tanzania*. Cambridge: Cambridge University Press.
- Jansen, B. D., Krausman, P. R., Heffelfinger, J. R., & de Vos, J. C. (2007). Influence of mining influence, on behavior of bighorn sheep. *Southwestern Naturalist*, 52, 418–423.
- Jetz, W., Wilcove, D., & Dobson, A. (2007). Projected impacts of climate change and land-use change on global diversity of birds. *PLoS Biology*, 5, 1211–1218.
- Kent, V. T. (2011). *The status and conservation potential of carnivores in semi-arid rangelands, Botswana. The Ghanzi farmlands: A case study* (Durham theses). Durham University. Available at Durham E-Theses online: <http://etheses.dur.ac.uk/728/>
- Kinnaird, M. F., & O'Brien, T. G. O. (2012). Effects of private-land use, livestock management, and human tolerance on diversity, distribution, and abundance of large African mammals. *Conservation Biology*, 26, 1026–1039.
- Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E. D., Clough, Y., et al. (2009). On the relationship between farmland biodiversity and land-use intensity in Europe. *Proceedings of the Royal Society B: Biological Sciences*, 276, 903–909.
- Kolowski, J. M., & Alonso, A. (2010). Density and activity patterns of ocelots (*Leopardus pardalis*) in northern Peru and the impact of oil exploration activities. *Biological Conservation*, 143, 917–925.
- Lawler, J. J., O'Connor, R. J., Hunsaker, C. T., Jones, K. B., Loveland, T. R., & White, D. (2004). The effects of habitat resolution on models of avian diversity and distributions: A comparison of two land-cover classifications. *Landscape Ecology*, 19, 517–532.
- Linnell, J. D. C., Odden, J., Smith, M. E., Aanes, R., & Swenson, J. E. (1999). Large carnivores that kill livestock: Do problem individuals really exist? *Wildlife Society Bulletin*, 27, 698–705.
- MacKenzie, D. I., & Bailey, L. L. (2004). Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, 9, 300–318.
- MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. P., Bailey, L. L., & Hines, J. E. (2006). *Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence*. New York: Academic Press.
- Maddock, A. H. (1988). *Resource partitioning in a viverrid assemblage* (Ph.D. thesis). Pietermaritzburg: University of Natal.
- Maddock, A. H., & Perrin, M. R. (1993). Spatial and temporal ecology of an assemblage of viverrids in Natal, South Africa. *Journal of Zoology*, 229, 277–287.
- Maitima, J., Mugisha, S., Reid, R., Gachimb, L., Majule, A., Lyaruu, H., et al. (2009). The linkages between land use change, land degradation and biodiversity across East Africa. *African Journal of Environmental Science and Technology*, 3, 311–325.
- Martinoli, A., Preatoni, D., Galanti, V., Codipietro, P., Kilewo, M., Fernandes, C. A. R., et al. (2006). Species Richness and habitat use of small carnivores in the Arusha National Park (Tanzania). *Biodiversity and Conservation*, 15, 1729–1744.
- Moreira, F., & Russo, D. (2007). Modelling the impact of agricultural abandonment and wildfires on vertebrate diversity in Mediterranean Europe. *Landscape Ecology*, 22, 461–476.
- Msuha, M. J., Carbone, C., Pettorelli, N., & Durant, S. M. (2012). Conserving biodiversity in a changing world: Land use change and species richness in northern Tanzania. *Biodiversity and Conservation*, 21, 2747–2759.
- Mulwa, R. K., Böhmig-Gaese, K., & Schleuning, M. (2012). High bird species diversity in structurally heterogeneous farmland in Western Kenya. *Biotropica*, 44, 801–809.
- Naro-Maciel, E., Sterling, E. J., & Rao, M. (2009). Protected areas and biodiversity conservation I: Reserve planning and design – Synthesis. *Lessons in Conservation*, 2, 18–48.
- Newmark, W. D. (1996). Insularization of Tanzanian parks and the local extinction of large mammals. *Conservation Biology*, 10, 1549–1556.
- Nummelin, M. (1990). Relative habitat use of duikers, bush pigs, and elephants in virgin and selectively logged areas of the Kibale Forest, Uganda. *Tropical Zoology*, 3, 111–120.
- O'Brien, T. G. (2008). On the use of automated cameras to estimate species richness for large- and medium-sized rainforest mammals. *Animal Conservation*, 11, 179–181.
- O'Brien, T. G., Kinnaird, M. F., & Wibisono, H. T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, 6, 131–139.
- Otis, D. L., Burnham, K. P., White, G. C., & Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monograph*, 62, 1–135.
- Parmenter, R. R., Brantley, S. L., Brown, J. H., Crawford, S. C., Lightfoot, D. C., & Yates, T. L. (1995). Diversity of animal communities on southwestern rangelands: Species patterns habitat relationships and land management. In N. E. West (Ed.), *Natural resources and environmental issues: Biodiversity on rangelands* (pp. 50–71). Logan: Utah State University.
- Pereira, H. M., Leadley, P. W., Proenca, V., Alkemade, R., Scharle-mann, J. P. W., Fernandez-Manjarres, J. F., et al. (2010). Scenarios for global biodiversity in the 21st century. *Science*, 330, 1496–1501.
- Pero, L. V., & Crowe, T. M. (1996). Helmeted guineafowl (*Numida meleagris*) in KwaZulu-Natal: A case for non-sustainability. *South African Journal of Wildlife Research*, 26, 123–140.
- Pettorelli, N., Lobora, A. L., Msuha, M. J., Foley, C., & Durant, S. M. (2010). Carnivore biodiversity in Tanzania: Revealing the distribution patterns of secretive mammals using camera traps. *Animal Conservation*, 13, 131–139.
- Pimm, S. L., & Raven, P. (2000). Biodiversity: Extinction by numbers. *Nature*, 403, 843–845.
- Pressey, R. L. (1996). Protected areas: Where should they be and why should they be there? In I. F. Spellerberg (Ed.), *Conservation biology* (pp. 171–185). Harlow: Longman.
- Ramesh, T., & Downs, C. T. (2013). Impact of farmland use on population density and activity patterns of serval in South Africa. *Journal of Mammalogy*, 94, 1460–1470.
- Ramesh, T., Kalle, R., Sankar, K., & Qureshi, Q. (2012). Spatio-temporal partitioning among large carnivores in relation to major prey species in Western Ghats. *Journal of Zoology*, 287, 269–275.
- Ramesh, T., Kalle, R., Sankar, K., & Qureshi, Q. (2013). Dry season factors determining habitat use and distribution of mouse deer (*Moschiola indica*) in the Western Ghats. *European Journal of Wildlife Research*, 59, 271–280.
- Remonti, L., Balestrieri, A., & Prigioni, C. (2011). Percentage of protein, lipids, and carbohydrates in the diet of badger *Meles meles* populations across Europe. *Ecological Research*, 26, 487–495.
- Rowcliffe, J. M., & Carbone, C. (2008). Surveys using camera traps: Are we looking to a brighter future? *Animal Conservation*, 11, 185–186.
- Rowe-Rowe, D. T. (1992). *The carnivores of Natal*. Pietermaritzburg: Natal Parks Board.
- Rowe-Rowe, D. T. (1994). *The ungulates of Natal*. Pietermaritzburg: Natal Parks Board.
- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloom-field, J., Dirzo, R., et al. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287, 1770–1774.

- Sarmento, P. B., Cruz, J., Eira, C., & Fonseca, C. (2011). Modeling the occupancy of sympatric carnivores in a Mediterranean ecosystem. *European Journal of Wildlife Research*, 57, 119–131.
- Schipper, J., Chanson, J. S., Chiozza, F., et al. (2008). The status of the world's land and marine mammals: Diversity, threat and knowledge. *Science*, 322, 225–230.
- Schuette, P., Wagner, A. P., Wagner, M. E., & Creel, S. (2013). Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation*, 158, 301–312.
- Soule, M. E., & Terborgh, J. (1999). *Continental conservation, scientific foundations of regional reserve networks*. Washington, DC: Island Press.
- SPSS. (2007). *SPSS for windows, version 16.0*. Chicago, IL, USA: SPSS.
- Thuiller, W., Broennimann, O., Hughes, G., Alkemade, J. R. M., Midgley, G. F., & Corsi, F. (2006). Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Global Change Biology*, 12, 424–440.
- Tobler, M. W., Carrillo-Percegué, S. E., & Powell, G. (2009). Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. *Journal of Tropical Ecology*, 25, 261–270.
- White, D., Minotti, P. G., Barczak, M. J., Sifneos, J. C., Freemark, K. E., et al. (1997). Assessing risks to biodiversity from future landscape change. *Conservation Biology*, 11, 349–360.
- Woodroffe, R. (2000). Predators and people: Using human densities to interpret declines of large carnivores. *Animal Conservation*, 3, 165–173.
- Woodroffe, R., & Ginsberg, J. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, 280, 2126–2128.
- Wretenberg, J., Part, T., & Berg, A. (2010). Changes in local species richness of farmland birds in relation to land-use changes and landscape structure. *Biological Conservation*, 143, 375–381.
- Yoccoz, N. G., Nichols, J. D., & Boulenger, T. (2001). Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution*, 16, 446–453.