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Predation by small mammalian carnivores in rural agro-ecosystems: An undervalued ecosystem service?

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Abstract

Africa is endowed with a diverse guild of small carnivores, which could benefit stakeholders by providing ecosystem services while fostering conservation tolerance for carnivores. To investigate the potential of small carnivores for the biological control of rodents within agro-ecosystems, we assessed both the ecological and social landscapes within two rural villages in the Vhembe Biosphere Reserve, South Africa. We employed a camera trapping survey underpinned by an occupancy modelling framework to distinguish between ecological and observation processes affecting small carnivore occupancy. We also used questionnaires to investigate perceptions of small carnivores and their role in pest control. We found the greatest diversity of small carnivores in land used for cropping in comparison to grazing or settlements. Probability of use by small carnivores was influenced negatively by the relative abundance of domestic dogs and positively by the relative abundance of livestock. Greater carnivore diversity and probability of use could be mediated through habitat heterogeneity, food abundance, or reduced competition from domestic carnivores. Village residents failed to appreciate the role of small carnivores in rodent control. Our results suggest that there is significant, although undervalued, potential for small carnivores to provide ecosystem services in agro-ecosystems.

1. Introduction

Rodents cause significant damage to crops in small-holder farms in Africa (Granjon and Duplantier, 2009; Monadjem *et al.*, 2015; Singleton, 2010; Swanepoel *et al.*, 2017). Existing rodent control is highly reactive and almost exclusively based on the use of rodenticides. This heavy reliance on poisons has led to increasing problems with the development of behavioural and physiological resistance, environmental contamination, and non-target poisoning (Buckle and Smith, 2015). Ecologically-based rodent management (EBRM) is a term popularised more than 20 years ago (Singleton *et al.*, 1999) with an aim to re-emphasize the importance of understanding rodent biology and behaviour of different species as well as agro-ecological and socio-economic contexts. While traditional rodent pest solutions emphasized over-reliance on poisons, EBRM advocates less harmful and sustainable solutions such as biological control through increasing ecosystem services of natural predation for pest control. Several studies have shown that the adoption of EBRM strategies for rodent pest management can be highly effective in reducing rodent damage whilst reducing farmer reliance on rodenticides (Brown *et al.*, 2006; Jacob *et al.*, 2010). EBRM has recently gained traction in small-holder agro-ecosystems in Africa (Massawe *et al.*, 2011; Monadjem *et al.*, 2015; Taylor *et al.*, 2012).

In smallholder agro-ecosystems, and many other modified landscapes, the removal of apex carnivore species from most human inhabited areas of Africa may have facilitated increased mesocarnivore abundance (Caro and Stoner, 2003; Prugh *et al.*, 2009; Ritchie and Johnson, 2009). Such increases might cause several ecological services or disservices to human communities. For example, small carnivores such as the red fox (*Vulpes vulpes*) provide valuable ecosystem services such as seed dispersal and potentially controlling populations of small mammals, regulating their impacts on keystone plant species and threatened habitats in Europe (Cancio *et al.*, 2017). In contrast, in Africa the importance of small carnivores around small-holder farming systems is well-recognised in terms of human-wildlife conflict and ecosystem disservices (Blaum *et al.*, 2009; Gusset *et al.*, 2009; Woodroffe *et al.*, 2005), but is less understood in terms of potential ecosystem services (Roemer *et al.*, 2009). This is unfortunate as Africa has a rich small carnivore assemblage, which could provide key ecosystem services to surrounding communities (Schuette *et al.*, 2013). Furthermore, the relatively large number of small-sized farms and small settlement areas in sub-Saharan Africa (Lowder *et al.*, 2016) are interspersed within a mosaic of semi-natural habitat that can increase human-wildlife conflict (Crooks, 2002; Lamarque *et al.*, 2009). As farm sizes in Africa are likely to continue to decline and further fragment the landscape (Masters *et al.*, 2013), there is a real risk of further natural habitat loss, trophic collapse and loss of potential ecosystem services provided by small carnivores (Dobson *et al.*, 2006).

Although the use of biological control is well established for many insect pests in agricultural production (Vincent *et al.*, 2007), it is not yet commonplace for rodent pests. The potential of avian predators to provide ecosystem services for the control of pest rodents has been recently reviewed (Labuschagne *et al.*, 2016), highlighting that some species, such as barn owls (*Tyto alba*), are able to control rodent pests in some in agricultural contexts. Recent research suggests that domestic cats and dogs may increase the landscape of fear around rural homesteads, resulting in lower rates of rodent activity and food intake (Mahlaba *et al.*, 2017). This indirect mechanism, affecting rodent behaviour, could work synergistically with direct control mechanisms such as predation of rodents by domestic carnivores, which could reduce rodent density (Krijger *et al.*, 2017). Little attention, however, has been given to the potential services or disservices of wild terrestrial carnivores in terms of rodent pest control.

Thus, the first objective of our study was to understand which small- and medium-sized mammalian carnivores (< 15 kg, hereafter referred to as small carnivores) were present in and around rural farming communities in the study area. Secondly, we set out to determine the influence of the abundance of domestic animals (livestock and pets) on the probability of use of an area by small carnivores; and also assess how the species richness of the small carnivore community was influenced by land use. Thirdly, we wanted to capture the knowledge and opinions of smallholder farming communities with respect to small carnivores. This will provide an initial yet essential step towards understanding the potential ecosystem services provided by small carnivores in rural agro-ecosystems, to help inform the development of EBRM strategies with a strengthened biological control component.

2. Methods

2.1. Study area

We conducted the study at two rural sites (Ka-Ndengeza: S23.31003° E30.40981° and Vyeboom: S23.15174° E30.39278°) in the Vhembe Biosphere Reserve, South Africa (Appendix S1). Both sites receive an annual rainfall of 700-800 mm per year, with a hot wet season from October to March and a cool dry season from May to August (Hijmans *et al.*, 2005). Natural vegetation is classified as Granite Lowveld and Gravelotte rocky bushveld

(Mucina and Rutherford, 2006). Vegetation is characterised by tall shrubs with few trees to moderately dense low woodland on the deep sandy uplands dominated by *Combretum zeyheri* and *C. apiculatum*. Low lying areas are characterised by dense thicket to open Savanna with *Senegalia (Acacia) nigrescens, Dichrostachys cinerea*, and *Grewia bicolor* dominating the woody layer, particularly the Granite Lowveld (Mucina and Rutherford, 2006).

Three major land-use types were identified in each of the villages. First, the settlement areas were used for residential purposes (hereafter settlements) (Odhiambo and Magandini, 2008). The majority of households had large gardens (50-80 m x 40-80 m) which were used to grow crops (maize (*Zea mays*), peanuts, beans (*Phaseolus vulgaris*), ground nuts (*Arachis hypogaea*), avocados mangoes, bananas, litchis, and oranges), and to overnight livestock (cattle, donkeys, sheep, goats, and poultry). The second land-use type identified was cropping areas (hereafter crops). Residents of both villages practiced either rotational cropping (maize, ground nuts, and beans) or intercropping (maize, beans, and pumpkins (*Cucurbita* spp.)). Land preparation was usually by manual labour, and preparation typically began in October or November, while planting commenced in early December. Harvesting of crops occurs in February until late April (crop dependant). Farmers reported yields varying between 5 to 20 bags (each bag weighing 50 kg) of maize and 3 to 10 bags of ground nuts (Swanepoel, unpublished data). Crop residues were typically used for livestock fodder. The third land-use type was the grazing areas, which comprised of short grass, shrubs and tall trees (hereafter grazing). In addition to communal grazing of livestock, these areas served for firewood collection and informal hunting. Due to poor land management practices, however, the grazing areas were typically severely overgrazed, with woody plants (mainly *Dichrostachys cinerea*) decreasing herbaceous production and replacing the grass and shrub layer, typically in low lying areas.

2.2. Potential small carnivore diversity and ecosystem services

We define predation of rodent pests and consumption of carrion as potential ecosystem services (Ćirović *et al.*, 2016) that could be provided by small carnivores. We estimated theoretical small carnivore diversity for our study sites by compiling a list of all small carnivore species potentially present at the study sites from the IUCN Red List of Threatened Species (IUCN, 2016) and from published literature (Apps, 2012; Cillié, 2013; Kingdon and Hoffman, 2012; Skinner and Chimimba, 2005; Stuart and Stuart, 2007). For each species we then extracted from the literature, data on the amount of rodents in their diets, and whether the species consumed carrion (Admasu *et al.*, 2004a, b; Apps, 2012; Camps, 2008; Cillié, 2013; Kingdon and Hoffman, 2012; Skinner and Chimimba, 2005). We regarded species with diets that included a minimum of 20% rodents as potential ecosystem service providers (Ćirović *et al.*, 2016). The home range size of the species potentially present, were used to determine the average distance between camera traps.

2.3. Camera trapping and data preparation

We used camera trapping to determine both species richness and habitat use (occupancy) of small carnivores. Our surveys were underpinned by an occupancy based modelling framework, which guided the layout of camera traps (MacKenzie and Bailey, 2004). Each study area was divided into a settlement area, cropping area and grazing area, based on recent satellite imagery (Google, 2014), which was then overlaid with a regular spaced grid with a cell size of 300 x 300 m (9 ha). The size choice of the grid cells was guided by the median home range size of small carnivores expected to inhabit the study areas (Table 1), to adhere to the independent assumptions of occupancy models (Mackenzie and Royle, 2005). We deployed one camera trap in each grid, which resulted in an average spacing between camera traps of 193 m (standard deviation 65 m), and camera traps were operated for 10-12 days. Camera traps were set to record 24 hours per day, with a 30 second delay between detections. We regarded individuals of the same species photographed within a 5-minute period as the same individual, to avoid pseudo-autocorrelation.

We deployed camera traps at roads, drainage lines, and well-established animal paths. We placed cameras around 30 cm above the ground, and cleared vegetation in front of camera traps to reduce the number of false triggers. In the settlement grid cells we deployed 27-30 infra-red flash cameras (Cuddeback Ambush 1194), as these were less disruptive to the inhabitants of villages than cameras using a visible light flash, while in the crops and grazing areas we deployed 55-60 xenon flash cameras (Cuddeback Ambush 1170). Camera traps were deployed between 2-26 June 2014 at Ka-Ndengeza and 17 June to 27 July 2014 at Vyeboom. This resulted in a camera trapping effort of 810 trap days in Ka-Ndengeza and 738 trap days in Vyeboom. From each camera trap we extracted detection-non-detection data for the target species, and calculated the relative abundance index (RAI) (O'Brien *et al.*, 2003) of other species we deemed important to the detection and occupancy of target species, such as domestic cats and dogs, livestock, and humans.

To classify land use we first digitized the different land-use types using satellite imagery from Google Maps (Google, 2014), which we later ground-truthed. This approach allowed us to plan the locations of our camera traps for optimal spacing, stratified by land use. We classified crops as either active fields, i.e. still showing agricultural activity, or as abandoned fields. For each camera trap we calculated the percentage of crops, grazing and settlement that comprised the camera trapping grid cell in which each camera trap was located. Camera trap images were catalogued using Camera Base version 1.7 (Tobler, 2015).

2.4. Questionnaires

We assessed the opinions of community members towards small carnivores using a structured questionnaire (Appendix S2) (based on the questionnaire used by Holmern and Røskaft (2014)), completed by a total of 127 respondents (n = 58 in Ka-Ndengeza and n = 69 in Vyeboom). For each camera trap the inhabitants of the nearest household were sampled, but when this was not possible another nearby house was selected. Photographs of small carnivore species were provided to ensure that the species were correctly identified. We asked interviewees whether they had seen each species of carnivore, if they were good for the community, if they kill rodents, if they had impacted the respondents negatively, and if they were aware if any small carnivore species that are killed by people. The reasons for any positive and negative impacts of the species were also recorded. We also asked whether interviewees consider poultry to be an important source of protein, in order to gain some insight into the motivations for farming chickens and protecting them by killing carnivores.

Ethical approval for the study was provided by the Ethics Committee of the University of Venda (approval number SMNS/14/ZOO/03/2803). We also obtained consent to interview community members of Ka-Ndengeza and Vyeboom from each community Chief in addition to community members. We informed each respondent that anonymity would be maintained, and obtained written consent from interviewees.

2.5. Data analysis

2.5.1. Community occupancy (probability of use) model

We used the MaoTau function in the EstimateS package (Colwell, 2016) to generate species accumulation curves to confirm sampling adequacy for the camera trap dataset (Gotelli and Colwell, 2011). We also used the camera trap data to estimate how the relative abundance of domestic animals influenced small carnivore occupancy, which can be defined as the proportion of the study site that was occupied by the study species (MacKenzie *et al.*, 2017). This is of interest because domestic animals could outcompete sympatric wild carnivores (Vanak and Gompper, 2009), reducing their capacity to provide ecosystem services. Due to the fact that little is known regarding home range and movement rates of South African small carnivores (Roemer *et al.*, 2009), we considered among-grid cell movement in small carnivore species a plausible violation of the closure assumption. As such the occupancy parameter (ψ) should be considered to represent the proportion of area used rather than the proportion of area occupied (MacKenzie and Bailey, 2004).

We adopted the hierarchical formulation of the Dorazio/Royle community occupancy model with data augmentation to estimate species-specific occupancy and site-specific species richness (Dorazio and Andrew Royle, 2005). In a single-species single-season occupancy model the probability that site j is occupied by species z_j is a Bernoulli random variable governed by the occupancy probability Ψ. The occupancy probability is modelled on the logit scale as either a function of site specific covariates or being constant. Analogous to occupancy, the probability that a species is detected is governed by the detection probability, p, which is conditioned on the true latent occupancy state, z_j. Survey sites are camera trapped on k occasions (e.g. days) where the observations, y_{jk}, is a Bernoulli random variable, either $p_{jk} = 1$ where $z_j = 1$ or p_{jk} 0 where $z_j = 0$. Detection probability is also modelled on the logit scale, either constant or as a function of site (e.g. vegetation type) or occasion (e.g. daily temperature) specific covariates.

We fitted community models to the data, as this allowed us to investigate the influence of the relative abundance of domestic animals on small carnivores at a community level (MacKenzie *et al.*, 2017). In the community model formulation the single-species single-season model is further extended where the latent and model parameters are indexed by species, *i*. This formulation results in a number of linked species-specific models because it is assumed that these species-specific parameters come from a common underlying distribution (governed by the hyperparameters, which in our study is the small carnivore community). To estimate the number species at each sampling site (including ones never detected) we augmented the data with all-zero observations for the hypothetical species (Dorazio and Andrew Royle, 2005). We hypothesized that in our study area a potential 23 small carnivore species could occur (IUCN, 2016), and we therefore augmented the observed data with 14 species.

We expected occupancy and diversity of small carnivores to be affected by various anthropogenic and environmental variables. To investigate these variables we developed an *a priori* model based on biological hypotheses on how small carnivore occupancy could be influenced by these variables. We hypothesized that small carnivore occupancy will be affected by the presence of domestic cat, dogs, livestock, humans and land use. Both domestic cats and dogs can either directly (through predation) or indirectly (through competitive exclusion) impact small carnivores (Brook *et al.*, 2012; Dickman, 1996). Similarly, humans can directly kill small carnivores (Berger, 2006; Ćirović *et al.*, 2016), and livestock can trample burrows of small carnivores and reduce vegetation cover (Blaum *et al.*, 2007a; Blaum *et al.*, 2007b). We used variance inflation factor (Zuur *et al.*, 2009) to identify and remove highly correlated variables to reduce multicollinearity. Using all the covariates we sequentially dropped the variable with highest VIF (however, we selected the variable with the least biological effect among variables with high VIF first), and recalculated the VIF until the VIF of each factor was below five (Zuur *et al.*, 2009). Using this approach we dropped percentage crops, settlement and grazing as these variables were highly correlated and had high VIF factors. Both human RAI and dog RAI were correlated and we thus dropped human RAI since we hypothesised that domestic dogs can have higher sustained impact on small carnivores (e.g. since dogs can roam over the landscape independent of humans).

We thus retained only domestic cat RAI, domestic dog RAI, and livestock RAI as explanatory occupancy covariates, and we modelled occupancy probability as having species-specific random intercepts with these three site covariates. We assumed that occupancy patterns were similar across villages, even though they were not sampled at the same time. For detection probability we only modelled the effect of survey date (Julian day) on detection, again as species-specific random intercept (Dorazio and Andrew Royle, 2005). We collapsed the 10-12 day survey into 5 sampling occasions to increase detection probabilities (Ramesh *et al.*, 2012), and each camera trap was regarded as independent.

We used a Bayesian framework (Plummer, 2003) to implement the community model. Full details can be found in Appendix S3, while the full model specification can be found in Appendix S4. Results are reported in mean, standard deviation and 95% Bayesian confidence intervals (95 BCI taken from the 2.5% and 97.5% percentiles of the posterior mean). We regarded coefficients as having strong inference value if its 95 BCI values did not include 0. We further estimated the number of small carnivore species per land use by summing the estimated species richness at each survey site, in each land use. Finally we used the estimated species richness at each camera trap location to create spatially explicit species richness maps using inverse distance weighted interpolation (Sarmento *et al.*, 2010). We used R v3.4.1 (R

Development Core Team, 2017) for all modelling, with the following R packages; raster for IWD (Hijmans, 2015), jagsUI (Kellner, 2016).

2.5.2. Questionnaires

The questionnaire data allowed us to investigate stakeholder perceptions of small carnivores in agro-ecosystems. We explored the questionnaire data by calculating the frequency with which respondents reported that 1) they had seen small carnivores; 2) small carnivores had either positive or negative impacts on people; 3) small carnivores kill rodents; and 4) people kill small carnivores. Some frequencies were represented graphically using bar plots created using the R package ggplot2 (Wickham, 2016). All data analysed in this study are publically available in Williams *et al.* (2017).

3. Results

3.1. Small and medium carnivore diversity and occupancy (probability of use)

Species accumulation curves plateaued at approximately 1,368 camera trapping days (8 survey days), which suggested adequate sampling (Appendix S5). Of 23 small and medium carnivore species potentially occurring at the study sites (IUCN, 2016), we detected 9 (8 at Ka-Ndengeza and 8 at Vyeboom) small carnivores representing 5 different families (Table 1). The mean metacommunity richness was estimated at 14.48 (95 BCI 9-22 species). However the mean metacommunity richness had a skewed posterior distribution and a wide credible interval. We therefore used the mode to estimate total metacommunity richness, which was estimated at 10.98 species.

The strength of associations with occupancy covariates varied between species (Fig. 1). The presence of cats did not have a strong association with any of the small and medium carnivore species, nor to the metacommunity as a whole (Fig. 1). In contrast, dogs had a strong negative association with occupancy probability (probability of use) for all species and the metacommunity (Fig. 1). For livestock only four species (white tailed mongoose, slender mongoose, Selous' mongoose, and large spotted genet) showed strong positive associations with livestock presence, while the other five species had no association. Interestingly, the metacommunity also had a strong positive association with livestock presence (Fig. 1).

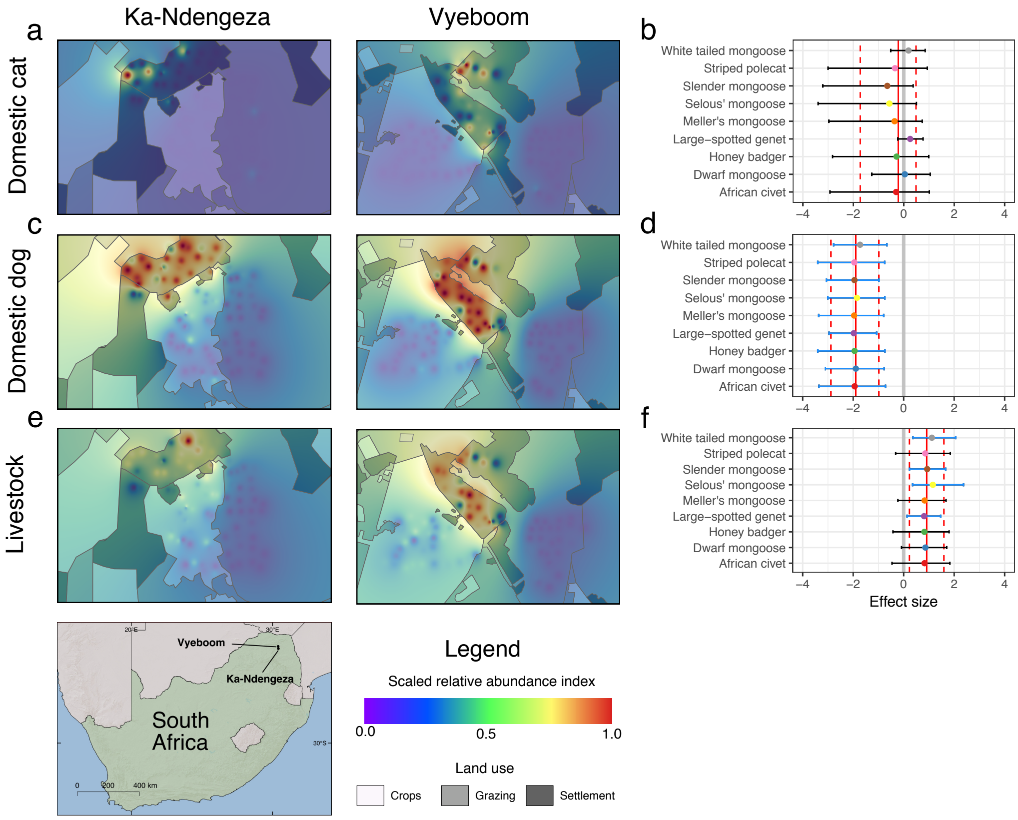

Fig. 1. Interpolated heat maps based on relative abundance index (scaled between 0 and 1) for a) domestic cat, c) domestic dog, and e) livestock across the settlement, crop, and grazing areas in Ka-Ndengeza and Vyeboom. Caterpillar plots show the strength of associations between the RAI of b) domestic cat, d) domestic dog, and f) livestock with occupancy (probability of use) of the nine carnivore species detected. Confidence intervals highlighted in blue do not overlap 0. The broken lines indicate the 95 BCI for the mean community response to each variable.

Cropping areas consistently showed higher species richness than grazing and settlement areas (Fig. 2). Spatially, species richness density surfaces clearly adhered to cropping areas and highest species richness per 900 m^2 grid cell were consistently observed in the cropping areas (Fig. 2). A survey of the literature showed that 65% of these species (15/23) are reported to have at least 20% of rodents in their diet (Table 1). Combined with species richness maps this suggests that the small and carnivore community not only occur most often in cropping areas, but also probably incorporate a large proportion of rodents in their diet. Using the mode small carnivore richness (10.98) as a reliable estimate of species richness we suggest that the study area realised around 47% of the potential small carnivore diversity.

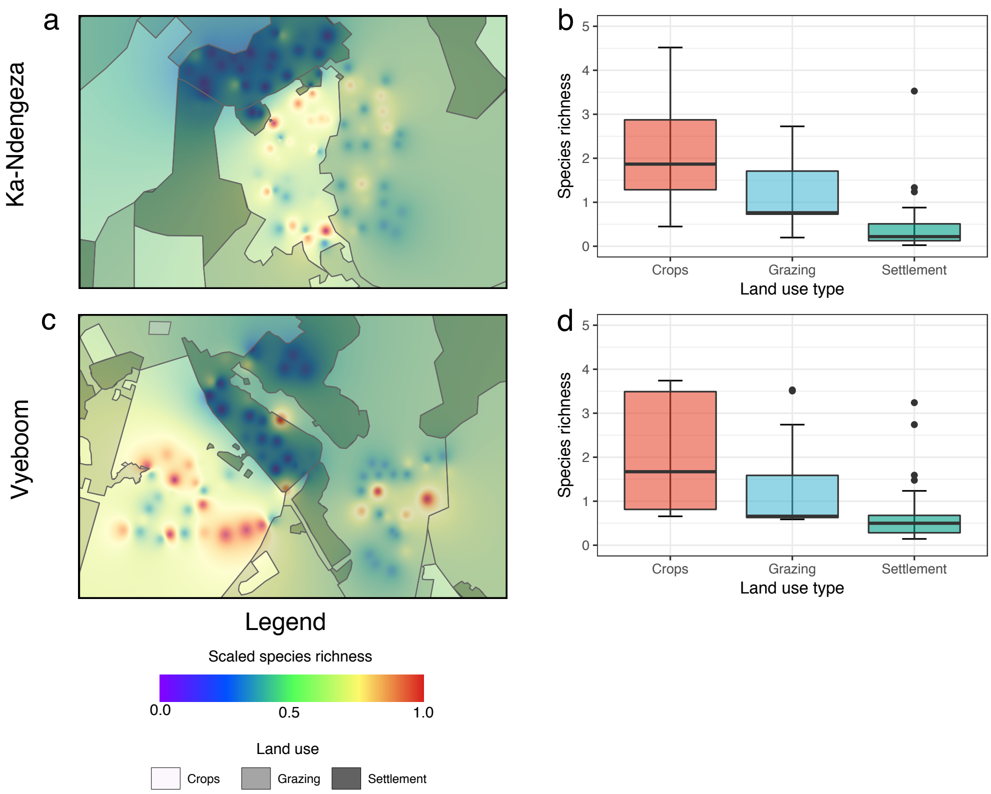

Fig. 2. Maps and boxplots showing how the species richness (scaled between 0 and 1) of small carnivores varies with land use at Ka-Ndengeza (a, b) and Vyeboom (c, d). Boxplots show mean number (posterior mean) of species estimated at each camera trap, summarized per land use.

Table 1. List of carnivore species detected during the camera trap study. The table is ordered according to family level (all capitals).

					Number of independent detections per 1,000 camera trap days						
					Ka-Ndengeza			Vyeboom			
Common name	Scientific name	Home range size (km^2)	Consumes carrion	% of scats or stomachs that contain rodent remains	Settlement	Crops	Grazing	Settlement	Crops	Grazing	IUCN Red List[5]
CANIDAE											
Domestic dog	*Canis lupus familiaris*				9324.1	1269.8	308.1	5160	201.7	37.04	
MUSTELIDAE											
Striped polecat	*Ictonyx striatus*	-	No	20-30[1]	0	0	5.1	0	8.23	0	Least concern
Honey badger	*Mellivora capensis*	10 - 30	Yes	30[1], 57[2]	0	0	0	0	0	6.17	Least concern
FELIDAE											
Domestic cat	*Felis catus*				324.07	0	10.1	720	0	6.14	
VIVERRIDAE											

Large-spotted genet	*Genetta maculata*	0.5 - 1	No	47[3], 68[4]	0	642.86	217.17	22.22	172.8	228.4	Least concern
African civet	*Civettictis civetta*	5 - 11.1	Yes	41[4]	0	0	0	0	8.23	0	Least concern
HERPESTIDAE											
Slender mongoose	*Galerella sanguinea*	0.5 - 1	Yes	25[3]	0	253.97	25.25	0	148.15	86.42	Least concern
Meller's mongoose	*Rhynchogale melleri*	-	No	Not available	0	47.62	0	0	0	0	Least concern
Selous' mongoose	*Paracynictis selousi*	-	No	Not available	0	71.43	0	0	32.92	0	Least concern
White tailed mongoose	*Ichneumia albicauda*	4 - 8	Yes	18[3]	0	150.79	0	26.67	8.23	18.52	Least concern
Dwarf mongoose	*Helogale parvula*	1 - 3	No	4	0	31.75	0	4.44	4.12	30.86	Least concern
Species richness	11				2	7	5	5	8	7	
% of potential maximum species richness (23)					9	30	22	22	35	30	

[1]Apps (2012)
[2]Skinner and Chimimba (2005)
[3]Smithers (1971)
[4]Smithers and Wilson (1979)
[5]IUCN (2016)

3.2. Questionnaires

Eleven species of non-domesticated small carnivore species were reported to be seen by the respondents (Appendix S6). All mongoose species (with the exception of water mongoose), African wildcat, small spotted genet, black backed jackal, and striped polecat were reported most frequently. African civet and honey badger were seen by few respondents, while caracal, serval, and water mongoose had not been seen. Domestic cats and domestic dogs had been seen by all interviewees. The only species perceived to benefit the community were domestic cats and domestic dogs (Table 2).

Table 2. Percentage of respondents (n = 58 in Ka-Ndengeza and n = 69 in Vyeboom) with positive responses to questions on interactions between carnivores and humans.

	Are they good for the community?		Do they kill rodents?		Do they impact you negatively?		Do people kill them?	
Species	Ka-Ndengeza	Vyeboom	Ka-Ndengeza	Vyeboom	Ka-Ndengeza	Vyeboom	Ka-Ndengeza	Vyeboom
Banded mongoose	0	0	0	15.9	20.7	43.5	0	0
Dwarf mongoose	0	0	5.2	15.9	32.8	95.7	1.7	1.4
Slender mongoose	0	0	25.9	15.9	89.7	79.7	8.6	0
Yellow mongoose	0	0	1.7	11.6	0	0	1.7	0
White tailed mongoose	0	0	3.4	15.9	22.4	72.5	0	0
Water mongoose	0	0	0	0	0	0	0	0
Black backed jackal	0	0	0	0	0	5.8	0	0
African civet	0	0	0	0	0	0	0	0
Small spotted genet	0	0	13.8	0	1.7	0	0	0
Striped polecat	0	0	27.6	0	0	0	0	0
Caracal	0	0	0	0	0	0	0	0
African wild cat	0	0	44.8	62.3	6.9	43.5	1.7	0
Honey badger	0	0	0	0	0	0	0	0
Domestic cat	51.7	98.6	100	100	6.9	1.4	0	0
Domestic dog	58.6	98.6	3.4	0	8.6	1.4	0	0

A total of eight species of non-domesticated carnivores were believed by some people to kill rodents (Ka-Ndengeza: seven species were thought to kill rodents by a mean of 17.5% of respondents; Vyeboom: six species were thought to kill rodents by a mean of 23.0% of respondents). The species most commonly thought to predate on rodents were African wildcat, striped polecat, and slender mongoose (Table 2).

Negative impacts of carnivores on people were reported for most mongoose species, black backed jackal, small spotted genet, and African wild cat (Table 2). Most negative impacts were perceived to be due to poultry predation, although a small number of respondents cited cultural reasons, such as involvement in witchcraft or other superstitions, for negative impacts (Appendix S7).

Slender mongoose, dwarf mongoose, yellow mongoose, and African wildcat were said to be killed by people (Table 2). The only reason provided for people killing carnivores was poultry predation. Poultry was considered to be an important source of protein by 98.3% of respondents in Ka-Ndengeza and 100.0% of respondents in Vyeboom. The median number of chickens owned was 10 (interquartile range = 13, n = 21) in Ka-Ndengeza, and 4 (interquartile range = 6, n = 24) in Vyeboom. Poultry were almost always free-ranging (in 96.6% and 100% of households surveyed in Ka-Ndengeza and Vyeboom respectively).

4. Discussion

Our camera trapping results indicated that cropping areas consistently supported the greatest diversity of small carnivores. Furthermore, the literature review showed that the small carnivore assemblages present typically incorporate a large percentage of rodents and carrion in their diets. Collectively these results highlight the potential for pest control and carrion removal by small carnivores as important ecosystem services. Our results concur with other studies that highlight the unrealised potential of small carnivore predation and scavenging as ecosystem services (Ćirović *et al.*, 2016; Mateo-Tomás *et al.*, 2015). Rodent pests, for example, account for approximately 15% of the damage caused to rural farming crops in Africa (Swanepoel *et al.*, 2017), and such damage is dependent on the density of rodents (Brown *et al.*, 2007). Since small carnivore diets include a large proportion of rodents, it is likely that small carnivore predation could be a key factor affecting rodent abundance, and therefore reduce crop damage (Ćirović *et al.*, 2016). Further support comes from meta-analysis studies, that show that reduced predation increases population growth for cyclic prey (Salo *et al.*, 2010) and provisioned populations of small mammals such as rodents feeding on grain (Prevedello *et al.*, 2013; Salo *et al.*, 2010). There therefore appears to be strong support, both from our findings and from the literature, that predation of rodents by small carnivores could be an important ecosystem service to rural communities through EBRM.

Our results showed that abundance of domestic dogs (and feral dogs) and livestock are important determinants of small carnivore diversity and habitat use, while cats seemed to have little effect. Several studies have highlighted the negative impact of dogs (domestic and feral) on native mammalian communities (Hughes and Macdonald, 2013; Reed and Merenlender, 2011). For example, dogs can act as intraguild competitors where they can outcompete carnivores, especially under conditions of low prey biomass (Vanak and Gompper, 2009). We suggest that such a scenario is most likely prevalent in rural African landscapes were local fauna often form part of the diet of people in rural areas (Holmern *et al.*, 2006). Furthermore dogs, especially when roaming freely (a scenario common in African rural landscapes (Czupryna *et al.*, 2016)), can kill small carnivores (Ralls and White, 1995). Finally, dogs are often used during hunting activities where they can kill non-target species such as small carnivores (Holmern *et al.*, 2006).

The lack of effect of cats on small carnivore occupancy is surprising, given the large impact cats have on mammalian communities (Loss *et al.*, 2013). We provide two possible reasons for this lack of effect; first cats most often include small mammals in their diet (Loss *et al.*, 2013), and as such might impact small carnivores through competitive exclusion (Brook *et al.*, 2012). However, densities of cats in our study might not be high enough to achieve such an effect.

Secondly, dog hunting often occurs at night (Holmern *et al.*, 2006), which might restrict cats (and hence their impact on small carnivores) to the settlement areas. The positive effect of livestock contrasts with other studies that highlight the negative impact of livestock on small carnivores (Blaum *et al.*, 2007a; Blaum *et al.*, 2007b). We hypothesised that this effect is probably mediated through invertebrate food sources for small carnivores. For example the four small carnivore species exhibiting a positive occupancy effect due to livestock (large spotted genet, slender mongoose, white tailed mongoose and Selous' mongoose) all incorporate a large proportion of invertebrates in their diet (Skinner and Chimimba, 2005). Studies have shown that disturbance-adapted insect populations increase in abundance in highly impacted areas (e.g. heavy grazed) (Schowalter, 1985; Seymour and Dean, 1999). Therefore, the presence of livestock can create local conditions of increased invertebrate biomass, which could facilitate small carnivore presence.

We found that cropping areas had the highest small carnivore richness, which contrasts with the low biodiversity often observed in intensive agricultural systems (Benton *et al.*, 2003). We provide several hypotheses for this observation, which are not necessarily mutually exclusive. First, rural agricultural landscapes are often structurally complex and heterogeneous (Donald, 2004) which seems to support higher animal diversity (Norris, 2008). Secondly, rural agricultural systems support a diverse and high rodent abundance, especially in our study areas (Belmain, 2006), which can support small carnivores (Blaum *et al.*, 2007b). While dogs had a large effect on small carnivores, the highest dog and cat activities were observed in the settlement areas, and to a lesser extent in the cropping areas, which suggests that competitive exclusion and competition with small carnivores (Glen and Dickman, 2005; Vanak and Gompper, 2010) is limited in agricultural areas. Finally livestock abundance was higher in cropping areas compared to grazing areas, which could have created favourable conditions for high biomass of disturbance-adapted insect populations that can act food resource for small carnivores (Seymour and Dean, 1999).

While our results support the hypothesis that small carnivores could provide ecosystem services, we highlight that such a service would not depend solely on diversity, but also abundance of small carnivores. Our results show that the majority of small carnivores had low relative abundance indices, which were likely to be below ecologically effective densities (Soulé *et al.*, 2005). Nonetheless, the small carnivore assemblage present in these rural agro-ecosystems can still fulfil basic ecological functionality of predation (Roemer *et al.*, 2009). Such functionality will be largely dependent on whether the small carnivore assemblages retained inherent functional redundancy (Roemer *et al.*, 2009; Suraci *et al.*, 2017). This is important since the ecosystem service provision can be greater if expressed through collective effects, where the sum effect of predation (from different carnivores) might exceed that of a single small carnivore (Suraci *et al.*, 2017). Our study shows that the system retained some functional redundancy, however a large number of rodent specialists (e.g. striped polecat) were not detected or occurred at low relative abundances. Their absence probably reflects the small carnivore assemblage responding to pressures and changes as a result of human modification to the landscape that exist around rural agro-ecosystems. These responses will inadvertently bring shifts and changes in ecosystem service delivery and provision, which, if not checked can ultimately only exist as simple linear food chain communities (Roemer *et al.*, 2009). Therefore facilitating or at least maintaining small carnivore functional redundancy should be a key conservation management action in rural African landscapes if ecosystem services are to be maintained. Changes in rural landscapes are dynamic, which could potentially allow for various species of small carnivores to persist in them (Melo *et al.*, 2013). However, to what extent these changes retain or enhance functional redundancy remains to be explored.

Encouragingly, community members were able to identify 11 native small carnivore species that should occur in their areas, although we recorded fewer species using camera traps (nine wild species, domestic cats and domestic dogs). Although respondents were aware of the presence of the study species in their villages, and many respondents acknowledged the presence of rodents in the diet of some wild small carnivore species, they lacked any appreciation of the ecosystem services that they could provide. Reports of negative impacts of small carnivores were commonplace, almost exclusively due to perceived poultry predation. In both villages keeping of poultry was very common, and almost all respondents asserted that poultry was an important source of protein in their diet. The threat of poultry predation was said to be the main motivation for small carnivores being killed by community members.

The mechanism by which some small carnivores were thought to predate on poultry was unconventional and unsubstantiated. Many community members believed that carnivores would intentionally trap the beaks of chickens in their anus, before breaking their necks. Although some species of small carnivores such as the African civet, small spotted genet, and large spotted genet have been known to predate on poultry (Kingdon and Hoffman, 2012), and in some cases levels of poultry predation by small carnivores can be high (Holmern and Røskaft, 2014), such perceptions illustrate that the perceived threats of predation may not always have a strong grounding in reality. Nevertheless, it appears that overcoming perceptions of poultry predation will be the key challenge in promoting the role of small carnivores as providers of ecosystem services. Our results could help to demonstrate to community members that wild small carnivores are more likely benefit them by controlling pests and removing carcasses than predate on their poultry. We note that the wording of the questionnaires (Holmern and Røskaft, 2014) could be improved upon to reduce bias. As an example, we suggest that in future studies asking respondents to rate their benefit of a carnivore species on a Likert scale would be less biased than asking if a species is good for the community (Morgan-Brown *et al.*, 2010).

Although our findings indicate that small carnivores could provide ecosystem services through pest control and waste removal in rural agro-ecosystems, we suggest that further research may help to characterise the impacts of small carnivores on the density and diversity of rodents in agricultural fields, the amount of crop damage caused by rodents, and the amount of carrion removed. The socio-economic implications on the livelihoods of people adopting these strategies would also be worthy of further study.

5. Conclusions

Our findings suggest that agricultural areas could be important refuges for small carnivores within modified landscapes, and these species are likely to be providing important ecosystem services in rural agro-ecosystems. We found that agricultural areas supported the greatest diversity of small carnivores. Livestock was linked to higher levels of occupancy (probability of use) of small carnivores, while the opposite trend was observed for domestic dogs, and domestic cats had no influence on carnivore occupancy. The small carnivore species present are reported in the literature to dedicate a considerable proportion of their diets to rodents, and consume carrion. Although community members could identify many small carnivore species, they appeared to be unaware of the ecosystem services that the small carnivores are likely to provide through EBRM and carcass removal. The perceived threat of poultry predation emerged as a key challenge in promoting the role of small carnivores as providers of ecosystem services.

6. Appendices

Appendix S1. Study area figure

Appendix S2. Interview schedule.

Appendix S3. Model description and parameter estimates of the community occupancy model applied to small carnivore camera trapping data from a rural matrix.

Appendix S4. Community model JAGS code used in the analysis.

Appendix S5. Species accumulation curves to show sampling adequacy.

Appendix S6. Percentage of respondents in Ka-Ndengeza and Vyeboom that reported seeing species of small carnivores.

Appendix S7. Reasons provided why carnivores have impacted respondents negatively for Ka-Ndengeza and Vyeboom.

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