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Alice Bernard, Chloé Guerbois, Lizette Moolman, Melanie A de Morney, Jan A Venter, et al.. Combining local ecological knowledge with camera traps to assess the link between African mammal life-history traits and their occurrence in anthropogenic landscapes. *Journal of Applied Ecology*, 2024, 61 (10), pp.2470-2482. 10.1111/1365-2664.14742 . hal-04741688

HAL Id: hal-04741688

<https://hal.science/hal-04741688v1>

Submitted on 17 Oct 2024

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RESEARCH ARTICLE

Combining local ecological knowledge with camera traps to assess the link between African mammal life-history traits and their occurrence in anthropogenic landscapes

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Université de Lyon 1; CNRS (through its Institute INEE)

Handling Editor: Matthew Struebig**Abstract**

1. Understanding what influences species and trait composition is critical for predicting changes in communities driven by landscape transformation.
2. We explored how life-history traits are associated with the persistence of mammal species in human-dominated habitats within the Garden Route Biosphere Reserve, South Africa. We combined data from a camera trap study and a local ecological knowledge-based survey in an integrated occupancy model to analyse species occurrence along a gradient of anthropogenic landscape transformation.
3. Results confirmed that mammal occurrence in human-modified habitats was related to specific life-history traits. Species with more specialist diets, as well as larger body mass species were more likely to stay in protected areas. Species with slow reproductive strategies occupied more natural areas.
4. Combining different monitoring methods enabled us to increase spatial coverage and mammal sighting numbers. This approach fostered research participation by various stakeholders, an important step for co-designing wildlife-friendly anthropogenic spaces.
5. *Synthesis and applications.* Integrating data from a standard ecological protocol and structured participatory citizen knowledge allowed us to identify the species functional traits associated with mammal species occurrence in anthropogenic landscapes at a local scale. These results advocate for wisely combining methods and will guide conservation-orientated land-use planning towards the protection of natural habitats in the Garden Route Biosphere Reserve. This methodological approach will enable managers and conservationists to use data obtained from diverse protocols and should catalyse the involvement of citizens in biodiversity monitoring and conservation.

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KEYWORDS

biodemographic strategy, conservation, diet diversity, human-wildlife coexistence, integrated occupancy model, mammal ecology, participatory research, wildlife monitoring

1 | INTRODUCTION

The human footprint, a measure of the human impact on terrestrial land, has increased globally during the past several decades (Venter et al., 2016), thus creating novel environments that confront wildlife with conditions not typically encountered in natural environments (Fleming & Bateman, 2018; Moll et al., 2021). Human-dominated habitats include new land-uses, roads, buildings, as well as increased levels of urban noise or artificial light, all of which affect wildlife occurrence (Fleming & Bateman, 2018). It has been shown that human activities along an urban–natural gradient often negatively affect species (Hulme-Beaman et al., 2016; McKinney, 2002; Moll et al., 2021). The human modification of environments potentially drives new niche partitioning and competition between species (Moll et al., 2021; Sévêque et al., 2020; Van Scoyoc et al., 2023), thus disrupting the functioning of ecological communities (Wang et al., 2015). Such modification can eventually lead to local species extinction (Grimm et al., 2008) as well as local overabundance (Pocock et al., 2004; Stenseth et al., 2003).

Globally, the community composition of species in human-modified environments tends to homogenize (Newbold et al., 2018), often towards ‘winner’ species, that is those able to adjust to the new conditions (Grimm et al., 2008). These winner species tend to not only do well, but often even better in these new environments than in their original habitats (Barrett et al., 2019; Fleming & Bateman, 2018). Anthropogenic landscapes, including urban habitats, can benefit certain wild mammals (Santini et al., 2019), like some mesocarnivore species (Louvrier et al., 2021; Wang et al., 2015), by offering new food sources, such as pets, livestock or human commensal species (Fleming & Bateman, 2018; Hulme-Beaman et al., 2016). Additionally, human-transformed habitats could concentrate prey around waterholes or artificial lighting, thus reducing foraging costs for predators (Fleming & Bateman, 2018). Alternatively, novel environments may provide the opportunity for some species to develop wholly new tactics to find easily accessible food; for example, some species, such as Chacma baboons (*Papio ursinus*), will begin to steal food from houses or rubbish bins (Bernard, Fritz, Dufour, et al., 2024; Hoffman & O’Riain, 2012; Mazue et al., 2023).

In the context of global human-induced terrestrial landscape transformation, it is necessary to understand which traits enable species to successfully use anthropogenic matrices. This will help to understand wildlife communities maintained in such environments (Hulme-Beaman et al., 2016). Mammals are a good model to study the effect of species traits on their capacity to use anthropogenic environments, as they represent a diversity of sizes, diets and ecological requirements (Santini et al., 2019), attract recreational interest (Okello et al., 2008) and are subject to experience tensions with humans (Kansky & Knight, 2014).

Several studies have illustrated how life-history traits determine species capacity to adjust to a new environment, which seems to vary between taxonomic groups and populations (Hulme-Beaman et al., 2016; Santini et al., 2019). Life-history traits, such as speed of reproduction or body mass, can thus explain species sensitivity to human footprints (Suraci et al., 2021). By repeatedly experiencing negative interactions with humans, some species can learn and modify their behaviour in order to avoid conflict (Barrett et al., 2019). Responding quickly to favourable conditions, adaptable species often exhibit demographic traits associated with the r-strategy (high fecundity and large litter size; Hulme-Beaman et al., 2016). Species considered invasive often breed rapidly, do not live long and occur at high densities (Hulme-Beaman et al., 2016; Pocock et al., 2004). Species with plasticity in habitat selection, feeding behaviour or diet (i.e. generalist or omnivorous) are also more likely to adapt and benefit from anthropogenic environments (Fleming & Bateman, 2018; Hulme-Beaman et al., 2016). Conversely, species with large spatial requirements (i.e. those most negatively impacted by habitat loss and fragmentation) are not expected to adapt well (Tucker et al., 2018). However, not all traits lead to consensual results; indeed, Wang et al. (2015) showed that the occurrence of pumas (*Puma concolor*), large, solitary carnivores, was lower in high-density residential areas, whereas leopards (*Panthera pardus*), a species with similar traits, perform well in the vicinity of humans (Athreya et al., 2013). This suggests that drivers of adaptability and persistence are complex.

A variety of methods can potentially be used to monitor mammal communities, combining them can provide complementary sets of information that mutually improve the understanding of certain phenomena, while increasing the spatial coverage and number of sightings (Schaller et al., 2012; Service et al., 2014). This often requires one to assess the limits and suitability of combining methods, as done for the combination of data acquired from interviews and camera traps (CTs) to better account for relative potential strengths and biases (Bernard, Guerbois, Venter, et al., 2024; Brittain et al., 2022; Burt et al., 2021; Martínez-Martí et al., 2016).

In this study, we integrated data from CTs and surveys based on local ecological knowledge (LEK) to explore how life-history traits influence wild mammal occurrence in the multifunctional anthropogenic landscapes of the Garden Route Biosphere Reserve (GRBR) in South Africa. We studied life-history traits associated with diet (type and diversity of resources consumed) and biodemographic strategy (longevity, gestation length, age at sexual maturity, litter size and body mass). First, we hypothesized that species with a generalist diet would be attracted to human-dominated habitats because of the availability of easily accessible food resources, while avoiding humans to limit negative encounters (Hulme-Beaman et al., 2016).

Second, we hypothesized that large carnivorous species would avoid human-occupied areas, which favour the presence of smaller carnivores and herbivores in the vicinity of humans (Berger, 2007; Suraci et al., 2021). Third, we hypothesized that species with long generation time (slow reproduction parameters) and large body mass would avoid modified landscapes, where adult mortality is highest, and therefore, would utilize natural habitats, corridors and less disturbed areas, making them more dependent on protected areas (Brennan et al., 2022; Santini et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in the GRBR, located on the south-eastern coast of South Africa, between the Indian Ocean and Outeniqua Mountains (Figure 1). Human-transformed landscapes are associated with multiple land-uses, such as commercial plantations, crops, dairy farming, urban and peri-urban development and road networks (Baard et al., 2015; SANParks, 2020). The Garden Route National Park (GRNP) is an unfenced protected area managed by South African National Parks (SANParks), tasked with protecting the rich biodiversity of a landscape that includes indigenous forests, fynbos, thickets, lakes, wetlands and marine habitats (Baard et al., 2015).

2.2 | Data collection

2.2.1 | Camera traps

Among a total of 74 CTs, 30 were set up within the GRNP and 45 in human-dominated areas (Figure 1). We deployed two models

of CTs: 33 Bushnell Trophy Cam HD Aggressor and 41 SPYPOINT Force Dark. The study contributed to the Snapshot Safari project (Pardo et al., 2021) where single CTs are positioned to detect medium to large mammals. To that end, a virtual grid of 5 km² (i.e. 2.23 × 2.23 km cells) was positioned on the landscape, between the towns of George and Knysna. Each CT was then positioned as close as possible to the centre of the grid cells, 50 cm above the ground, mainly in trees (Bernard et al., 2023). Each CT was programmed to take a series of three images within 1–5 s intervals. The CTs were checked every 2–3 months to replace their batteries and SD cards. The data were collected between February 2, 2021 and May 20, 2022. Four cameras were stolen during this period, but were not replaced because of the risk of repeated theft. No ethical approval was required due to the method being non-invasive.

2.2.2 | Online survey

We designed an online survey to gather additional data on species occurrence in human-dominated landscapes (Appendix S1). This protocol was granted ethics clearance by the Nelson Mandela University Human Research Ethics Committee (H20-SCI-SRU-002). The survey targeted residents of the GRBR. After the survey was piloted and revised, it was sent to prospective participants using mailing lists obtained from CapeNature, SANParks, the Wildlife and Environment Society of South Africa, local conservancies as well as WhatsApp and Facebook groups. Additionally, the survey link was published in local newspapers. The survey was available in English and Afrikaans and was accessible online from November 2021 to March 2022.

First, a written consent was required to start the survey (Appendix S2). Participants were then asked to indicate their residential location on a grid of 2.23 × 2.23 km cells on a map that

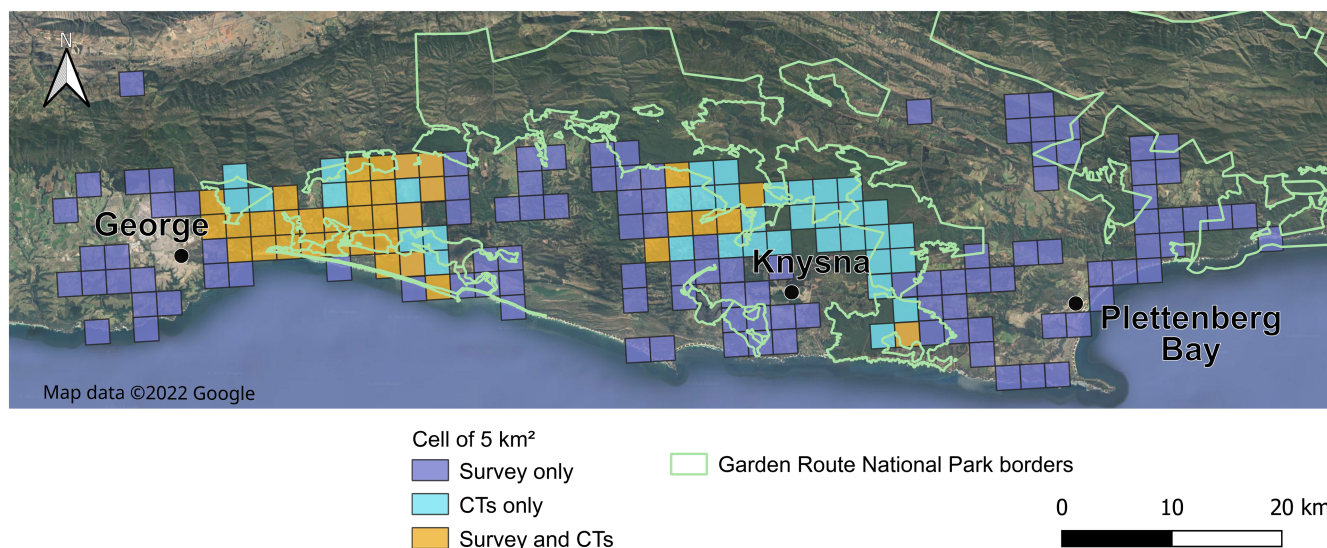


FIGURE 1 Study area in the Garden Route Biosphere Reserve, South Africa, showing a grid of 5 km² cells representing data from surveys only, camera traps (CTs) only and surveys and camera traps combined.

corresponded to the distribution of the CTs (Figure 1). Exact GPS locations were not required, thus preserving the anonymity of the participants. The presence of a given species was assessed based on how frequently respondents observed a species on their properties over the past 3 years: not anymore, rarely, occasionally, frequently or very frequently. Respondents were given the choice to select the generic categories of 'mongoose' or 'genet' when they did not know the differences between these species.

The ecological knowledge of respondents was tested using four questions. Two were based on identifying two respective species using a photograph: a herbivore (blue duiker; *Philantomba monticola*) and a mesocarnivore (Cape grey mongoose; *Galerella pulverulenta*). The third required respondents to identify the track of a carnivore (caracal; *Caracal caracal*), and the fourth to identify the scat of an herbivore (porcupine; *Hystrix africae australis*). For each question, respondents were given a choice of three species. Additional information about respondents was gathered from their responses to questions about their main activities, involvement in conservation initiatives and their properties. A more detailed description of the survey is given by Bernard, Fritz, Dufour, et al. (2024).

The research for the CT and the online survey was approved by SANParks (BERN-A/2020-008) and CapeNature (CN44-87-16198).

2.3 | Data processing

2.3.1 | Estimating mammal presence

Camera traps

The photographs of all detected species were manually tagged, first using digiKam (digiKam Team, 2001) and then the online software TrapTagger (Osner, 2022). All species detected were tagged; however, for this analysis, we focused on mammal species with a mass greater than 500g and disregarded all the other photographs. We created a detection matrix for each mammal species, grouped by 7 days, resulting in 16 survey occasions, to have enough detections for rare species (Niedballa et al., 2016). When the species was detected during the 7 days occasions, we considered it was a presence and added a 1, when it was not detected, we considered it was an absence and recorded a 0. We only considered the detection that occurred between the period from June 2021 to August 2021, to ensure the assumption of population closure (i.e. that no migration and immigration of individuals) required in occupancy analysis (MacKenzie et al., 2017). We selected this period to be sure that data from the online survey overlapped those from the CTs survey. This would not have been the case if we took a 3-month window in our data from the field periods comprised between October 2021 and May 2022.

Online survey

During the survey, respondents indicated the frequency at which they detected each species. If a respondent did not detect a given

species or reported that the species no longer occurred on their property, we assigned the variable a value of 0 (absence). Rare occurrence and occasional occurrence were assigned a score of 1 and 2, respectively. When a species was reported to occur frequently or very frequently, we assigned it a score of 3. To obtain a presence/absence variable for each respondent, the sightings from rare to very frequent were considered as presence, and no observation remained an absence. When there were several respondents in the same grid cell, we considered each respondent observation as a replicated detection, such as in the CTs detection matrix. Although two genet species were listed as potentially occurring in the area (Baard et al., 2015), only the large-spotted genet had been recently detected using CTs. Therefore, we interpreted responses using the general category 'genets' to refer to the large-spotted genet. In the case of mongooses, we only considered sightings from respondents who specified the species occurring on their properties, and excluded those using the general category 'mongooses' from subsequent analyses.

2.3.2 | Describing anthropogenic transformation of the landscape

To assess environmental conditions, we calculated variables to characterize anthropogenic landscapes at the scale of the 2.23 × 2.23 km cell. Using a shapefile of protected areas provided by SANParks (Baard et al., 2015), which we rasterized using QGIS, we calculated the percentage of protected areas in each cell. We then calculated the percentage of forest, fynbos, thicket and wetland habitats in each cell. This was done by summing the number of pixels of each land cover type, based on the 2020 South Africa National Land Cover Datasets (Department of Forestry, Fisheries and the Environment, 2020). We finally summed the percentages of the previously cited habitats, coming from the same raster layer, to calculate the overall percentage of natural habitats in each cell. To describe anthropogenic land cover, we created the 'cultivated areas' variable, calculating and summing the percentage of cultivated land, pastures and orchards, using the same methods and datasets (Department of Forestry, Fisheries and the Environment, 2020). To determine the potential impact of human footprint, we first calculated the mean human modification index (HMI) value per cell, which represents the level of modification of the land due to anthropogenic stressors (Kennedy et al., 2020). We then calculated the total length of roads (concrete and dirt) per cell to assess the potential disturbance associated with its human footprint (OpenStreetMap, 2022).

2.3.3 | Species life-history traits

We selected life-history traits that we expected to affect the probability of mammal species presence in anthropogenic environments. We used the EltonTraits database (Wilman

et al., 2014) to collate data on the diet of each detected species. Based on the work of Santini et al. (2019) and Suraci et al. (2021), we calculated the Shannon Index to estimate the dietary diversity of each species, based on the following diet categories: plants, seeds, fruits, scavenging, other vertebrates, fish, reptiles, mammals/birds and invertebrates. We completed our life-history trait dataset using the PanTHERIA database (Jones et al., 2009) to extract traits related to the biodemographic strategy of each species. The traits selected from this database were litter size, gestation length, age at sexual maturity, longevity, home range size and adult body mass. Species trait information is presented in Table S1.

2.4 | Data analysis

2.4.1 | Species characterization

We tested the correlation between each variable describing diet and biodemographic strategy, respectively, before conducting principal component analyses (PCAs) on trait variables (Figures S1 and S2). We used non-highly correlated variables ($r < 0.7$) and removed the variable 'group size', as it correlated with longevity and age at sexual maturity (Figure S2). We conducted two separate PCA: one on biodemographic strategies and one on dietary data (Dray & Dufour, 2007). We kept the first two axes of the PCA on diet, which accounted for 66.55% of the variation between species (Figure S2 and Tables S2 and S3). The aim of this approach was to create synthetic variables to reduce the number of traits to test and describe the species along gradients of traits. We extracted the three first axes of the PCA on biodemographic strategy, which accounted for 90% of the variation between species (Figures S4 and S5 and Tables S4 and S5). We used these five synthetic variables from the two PCAs to describe species traits and assess their relationships to the different anthropogenic variables described in Section 2.3.2.

2.4.2 | Species responses to anthropogenic variables

To make inferences about factors driving habitat use by species, we analysed the data in a Bayesian hierarchical framework. We ran the same single season, single-species occupancy model for each species using the spOccupancy package and the *intPGOcc()* function (Doser et al., 2022). We integrated presence/absence data from the CTs and online survey and corrected for the detection bias. We calculated a probability of detection for each dataset using two separate formula and used the same formula of occupancy (Doser et al., 2022).

Estimating the probability of detection p

For data from the CTs, we first controlled for variables which could explain heterogeneity in the detection of the species between the sites:

(1) the visibility in front of the CT, measured as the distance from the camera to the surrounding brush using a rangefinder; (2) the model of the CT (Spypoint or Bushnell); and (3) whether the CT was on a road, on a trail, on a game trail or outside of any identified trail. The probability of detection was given by (with i being the different cells):

$$\text{logit}(p_i) = \beta_{0i} + \beta_1 \text{Visibility}_i + \beta_2 \text{Model}_i + \beta_3 \text{Trail}_i$$

To consider the level of reliability provided in responses to the survey, we allocated each respondent a knowledge score based on their percentage of correct answers to the four ecological knowledge questions. We thus obtained a variable for each respondent between 0%, wherein no answer was correct, and 100%, wherein all the answers were correct. We included respondents with a local knowledge of 0% because their personal local knowledge might be based on shared observations made by someone else rather than their own experience. We hypothesized that the frequency of occurrence indicated by the respondents could also influence the certainty of presence or absence of a species. A species seen every day is more likely to be present than a species seen once. To correct for respondents' detection bias, both variables (1) the ecological knowledge score and (2) the frequency of detection of a species (between 0 and 3), were considered as detection variables. The probability of detection was given by (with i being the different cells and j the different respondents in a cell):

$$\text{logit}(p_{ij}) = \beta_{0ij} + \beta_1 \text{Knowledge}_{ij} + \beta_2 \text{Frequency}_{ij}$$

Estimating the probability of occupancy ψ

We first tested the correlation between the five anthropogenic candidate variables described in Section 2.3.2: percentage of natural habitats, cultivated areas and protected areas, HMI and road density. Road density and HMI were highly correlated ($r = 0.73$); thus, we decided to retain HMI for subsequent analysis (Figures S6 and S7). For the three percentage variables (natural habitats, cultivated areas and protected areas), we used the arcsine square root transformation to account for the percentages being skewed towards 0%, derived from Sokal and Rohlf (1981). In order to compare their effects, we scaled four variables for the purposes of modelling: percentage of natural habitats, cultivated areas and protected areas and HMI. For each species, we ran a single model, including all four previously described variables in the model and integrating data from the CTs and the online survey. The same occupancy model was used for each species to be able to compare their responses to each variable. Hence the probability of habitat use was given by the following function (with i being the different cells):

$$\text{logit}(\Psi_i) = \alpha_0 + \alpha_1 \text{Cultivatedareas}_i + \alpha_2 \text{Naturalhabitats}_i + \alpha_3 \text{Protectedareas}_i + \alpha_4 \text{HMI}_i$$

For each model, we ran three Hamiltonian Monte Carlo (HMC) chains with 8000 iterations, and used a burn-in of 3000 and a thinning rate of 25 (Kéry & Schaub, 2012). Using the Bayesian posterior distribution of the coefficient estimate, we determine whether

variables had a positive or negative effect on site occupancy for a given species. We considered variables to have a significant effect when the 95% credible interval (CI) of the estimate did not overlap zero. Finally, we calculated the Bayesian p -value for to ensure the fit of the models, using Freeman–Tukey statistic test and a Chi-squared test both on the detection and the occupancy models (Doser et al., 2022). We detected a Bayesian p -value between 0.1 and 0.9 for the detection model for the survey, indicating a correct fit of the models but a Bayesian p -value <0.1 for eleven species for the CTs, indicating a poor fit for the detection models (Table S6). To improve the fit, we tested various combination of detection variables for the CTs detection models but it did not improve the fit. We kept the initial detection model as default (i.e. with the variables: visibility, model and trail). We detected a Bayesian p -value between 0.1 and 0.9 for all the occupancy models, indicating a correct fit of the models (Table S6).

2.4.3 | Comparison of traits selected by anthropogenic pressures

From the single season, single species-integrated models, we extracted the estimates per species as a function of the following anthropogenic attributes: percentage of natural habitats, percentage of protected areas, percentage of cultivated areas and HMI. These estimates represent the change in log-odds occupancy per unit increase in each variable, which we consider reflect the probability of habitat use for a given species. We then ran a linear model following a normal distribution, using the estimate of species habitat use probability and the variables describing the life-history traits of each species as explicative variables. To take into account the error associated with each estimate, we included the uncertainty as weights in the linear models so estimates with lower uncertainty are given more weight. This allowed us to describe the change in likelihood of species presence in the landscape as a function of its trait values.

All the analyses were performed on R (R Core Team, 2020). We used the package 'ggplot2' for graphical representation and represented the regression lines and confidence intervals (Wickham, 2016).

Ethics approval statement

The research was approved by Nelson Mandela University Human Research Ethic Committee (H20-SCI-SRU-002), SANParks (BERN-A/2020-008) and CapeNature (CN44-87-16198).

3 | RESULTS

In total, we analysed 12,002 independent photos of wild mammal species and 235 completed surveys, describing 173 cells. Sixteen species were detected combining both methods; only the common duiker (*Sylvicapra grimmia*) was not detected by the CTs (Table 1).

The bushbuck (*Tragelaphus scriptus*) was the most common species, detected in 86% of cells, followed by the vervet monkey (*Cercopithecus pygerythrus*; 72%), porcupine (*Hystrix africae australis*; 69%) and chacma baboon (*Papio ursinus ursinus*; 68%). In contrast, the African clawless otter (*Aonyx capensis*; 20%), leopard (*Panthera pardus*; 22%) and Cape grysbok (*Raphicerus melanotis*; 22%) were the least widespread.

3.1 | Species responses to anthropogenic variables

In describing species responses to the anthropogenic environment, we only considered variables that had a significant effect (Figure 2 and Table S7). Out of 16 species, the porcupine was the only species to use more areas with more human modification (high HMI; Figure 2). No species showed a preference in habitat use regarding the percentages of cultivated area (Figure 2). The porcupine, bushbuck, baboon and genet were more likely to use areas with a lower percentage of natural habitats (Figure 2). The small grey mongoose was less likely to use cells with high percentages of protected areas (Figure 2). The effect of detection variables was species-specific, especially for the CTs (Table S8). Regarding the survey, the detection generally increases with the frequency of observation and the knowledge score of the respondents (Table S8).

3.2 | Species traits characterization

















The results of the PCA of diet showed that species present in the GRBR were spread along two gradients: (1) of specialist and generalist species on the first axis, labelled 'generalist diet' and (2) of carnivorous and herbivorous species on the second axis, labelled 'degree of herbivory' (Figure S2).

The results of the PCA of biodemographic strategy revealed three gradients: (1) generation length on the first axis, with slow reproduction (high longevity, late age at first reproduction and long gestation length) on one end and fast reproduction (including larger litter sizes) on the other (Pacifi et al., 2013); (2) the second axis of the PCA separated species with long gestation to those with older age at sexual maturity, that we called trade-off between gestation length and age at sexual maturity and (3) body mass on the third axis (Figures S2 and S5, Tables S4 and S5).

3.3 | Comparison of traits selected by anthropogenic pressures

The selection of species traits was only influenced by the percentage of protected areas and of natural habitats (Figure 3, Table S8). Cells with more protected areas selected for species with a more specialist diet (p -value=0.0499; Figures 3 and 4a, Table S9). Increasing percentage of protected area led to an increase in the probability of having species with large body mass (p -value=0.0366; Figures 3

TABLE 1 Summary of the detection of 16 species (icons downloaded from www.phylopic.org).

| English common name | | Scientific name | IUCN ^a red list category | Diet | Percentage of cells with species presence |
|--|---|----------------------------------|-------------------------------------|--------------------|---|
| Bushbuck |  | <i>Tragelaphus scriptus</i> | LC ^b | Herbivore | 86% |
| Vervet monkey |  | <i>Cercopithecus pygerythrus</i> | LC | Omnivore | 72% |
| Cape porcupine |  | <i>Hystrix africaeausalis</i> | LC | Herbivore | 69% |
| Chacma baboon |  | <i>Papio ursinus ursinus</i> | LC | Omnivore | 68% |
| Bushpig |  | <i>Potamochoerus larvatus</i> | LC | Omnivore | 66% |
| South African large-spotted genet (Cape genet) |  | <i>Genetta tigrina</i> | LC | Strict carnivore | 61% |
| Caracal |  | <i>Felis caracal</i> | LC | Strict Carnivore | 53% |
| Honey badger |  | <i>Mellivora capensis</i> | LC | Flexible carnivore | 46% |
| Cape grey mongoose |  | <i>Herpestes pulverulentus</i> | LC | Flexible carnivore | 39% |
| Common duiker |  | <i>Sylvicapra grimmia</i> | LC | Herbivore | 27% |
| Water mongoose |  | <i>Atilax paludinosus</i> | LC | Flexible carnivore | 26% |
| Large grey mongoose |  | <i>Herpestes ichneumon</i> | LC | Flexible carnivore | 24% |
| Blue duiker |  | <i>Philantomba monticola</i> | LC | Herbivore | 24% |
| Cape grysbok |  | <i>Raphicerus melanotis</i> | LC | Herbivore | 22% |
| Leopard |  | <i>Panthera pardus</i> | VU ^c | Strict carnivore | 22% |
| African clawless otter |  | <i>Aonyx capensis</i> | NT ^d | Flexible carnivore | 20% |

^aInternational Union for Conservation of Nature.

^bLeast Concern.

^cVulnerable.

^dNear Threatened.

and 4b, Table S9). Cells with higher percentage of natural habitats selected for species with higher values of trade-off between gestation length and age at sexual maturity (p -value=0.041; Figures 3 and 4c, Table S9). The degree of herbivory, home range size, generation length and the trade-off between gestation length and age at sexual maturity were not selected for by landscape variables (Figure 3). However, species with higher generation length and a more herbivory diet tended to prefer cells with a higher percentage of protected areas (p -value=0.0848 and p -value=0.11977, respectively; Figure 3, Table S9). Species with less herbivory diet (i.e. a more carnivore diet), seemed to select for cells with more natural habitats (p -value=0.0986; Figure 3, Table S8).

4 | DISCUSSION

Reliable information on mammal use of anthropogenic landscapes is crucial to developing appropriate conservation measures. By

combining CT and LEK data, we were able to increase the spatial coverage of our study area to describe the traits allowing mammals to persist in the multifunctional landscape of the GRBR. Sixteen mammal species above 500g in mass, cited in the mammal list of species of the GRNP (Baard et al., 2015), were detected in the diverse habitats of this mosaic landscape, with the exception of elephants (*Loxodonta africana*), with only one individual remaining (Moolman et al., 2019). Our results showed that protected areas play a crucial role in preserving large-bodied species and species with a more specialist diet, although a diversity of species was detected across the landscape. They also proved the importance of natural habitats in preserving species with high values of trade-off between gestation length and age at sexual maturity, that is species with a slow demographic strategy. This echoes the results of other studies on the failure of some species to inhabit more urban areas (Santini et al., 2019). We highlighted the value of integrating different datasets, especially to document the presence rare and cryptic species such as the common duiker or the African clawless otter.

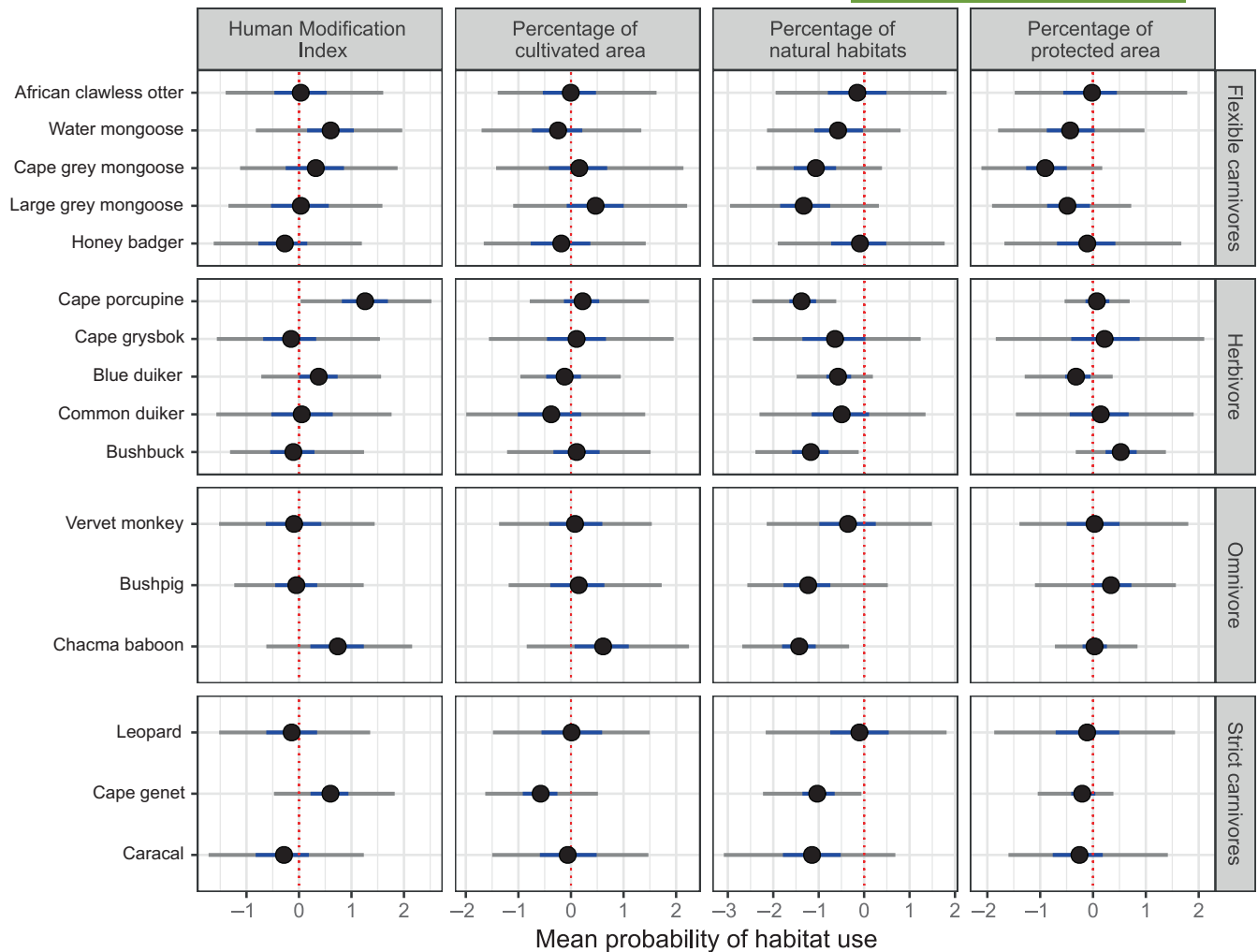


FIGURE 2 Mean probability of species habitat use in relation to landscape variables, obtained from generalized linear models. Species are sorted by diet type. Grey lines represent the 95% credible interval and blue ones the 50% credible interval. Red lines highlight the position of zero on the x-axis. Positive values represent a positive relationship between species occurrence and a given landscape variable and vice versa. The further away from zero the estimate, the stronger the landscape's effect on species occurrence (as variables are scaled).

Species with a generalist diet were less likely to use cells with a high percentage of protected areas than other species. This result was expected, as areas highly modified by humans usually do not favour species with very specialized diets and protected areas are their last refuge (Hulme-Beaman et al., 2016; Santini et al., 2019). Although we did not detect this effect, several studies had suggested that generalist species could take advantage of the diversity of new resources available in human-modified landscapes, such as refuse or crops (Hulme-Beaman et al., 2016; Santini et al., 2019). As such, we would have expected species with a more generalist diet, such as Primates, to take advantage of cells with a higher percentage of agricultural areas or with high value of HMI. Further, we detected that species in cells with higher percentage of protected areas tended to have a more herbivore diet. Studies have suspected that carnivores may take advantage of the commensal species found in anthropogenic landscapes, which could be the case for the carnivores of our study (Fleming & Bateman, 2018; Hulme-Beaman et al., 2016).

Species with higher body mass likely occupy cells with a high percentage of protected area because they require landscape connectivity and are vulnerable to habitat fragmentation (Brennan et al., 2022). Large carnivore species, such as the leopard and caracal of this study, probably avoided humans in highly modified areas because of conflict and rather stayed in protected areas (Carter & Linnell, 2016; Zimmermann et al., 2020). Avoiding direct encounters might help to reduce potential negative interactions (Barrett et al., 2019). The relative absence of large top predators (leopards and caracals) in highly modified areas could explain why smaller species such as mesocarnivores are favoured, as they likely benefit from human presence as a shield to lower the risk of predation (Berger, 2007) while also using anthropogenic resources. Small species could also be more secretive or less intimidating than larger carnivores and thus more tolerable to people (Carter & Linnell, 2016; Treves & Bruskotter, 2014). Smaller species might perform better in habitats modified by humans because of their ability to avoid

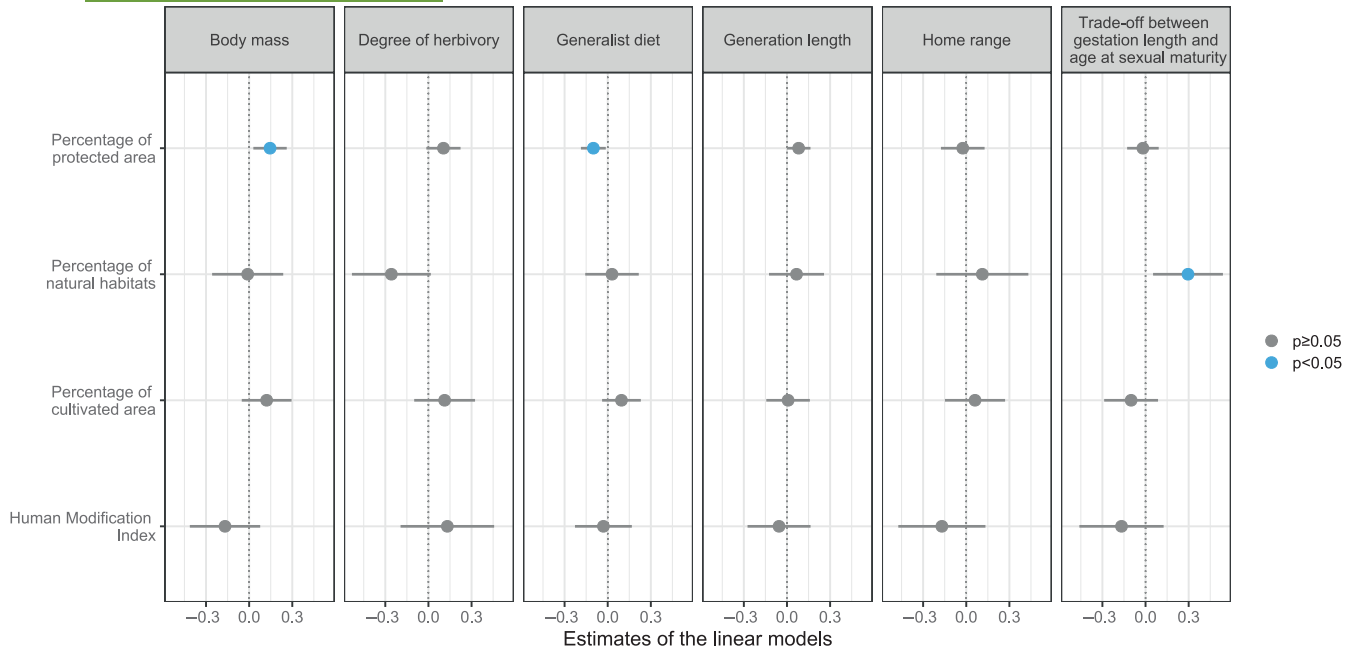


FIGURE 3 Estimates of the linear models obtained from the mean probability of species habitat use as a function of species traits, obtained from linear models. Significant estimates are represented in blue and non-significant estimates in grey. The grey lines represent the standard deviation multiplied by 1.96.

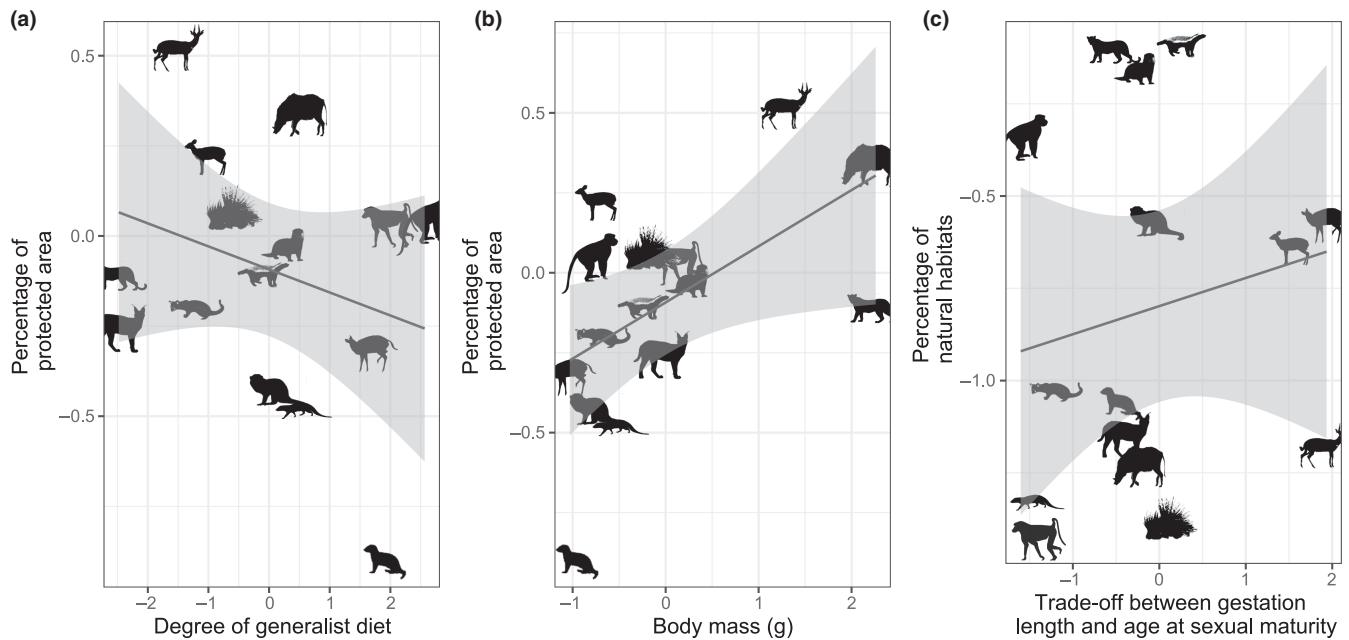


FIGURE 4 Estimates of species occurrence obtained from linear models as a function of traits significantly related to landscape variables. (a) Degree of generalist diet in relation to the percentage of protected area. (b) Body mass in relation to the percentage of protected area. (c) Trade-off between gestation length and age at sexual maturity in relation to the percentage of natural habitats. Species are represented using their associated symbols in Table 1.

anthropogenic threats (Suraci et al., 2021). These results are consistent with those found in the literature such as the selection of smaller species with faster life history were selected in areas with higher human footprint in the USA (Suraci et al., 2021). It is also possible that herbivores could use human-modified areas to benefit from human shield against large predators (Berger, 2007), but we found no evidence for this.

Traits related to a slower reproduction strategy (high values of trade-off between gestation length and age at sexual maturity) were selected in cells with higher percentage of natural habitats. This trend is confirmed by other studies, which showed that species with lower reproduction strategies were not favoured in highly modified landscapes (Santini et al., 2019; Suraci et al., 2021). Similarly, species with higher generation length tended to be more

present in cells with higher percentage of protected areas. Our results suggest that maintaining refuge areas (formally protected or not) is critical to conserve the diversity of traits in mammal communities at the landscape level. Our results concur with those of other studies in urging to preserve protected areas and natural habitats within mosaic landscapes to conserve the largest diversity of species (Downs et al., 2021; Grass et al., 2019). The active design of wildlife-friendly areas within modified environments could play a major role in conserving biodiversity in anthropogenic landscapes, while allowing opportunities for reconnecting people to nature (Lovell & Johnston, 2009; Obura et al., 2021; Rosenzweig, 2003).

Human modifications did not select for a particular type of species, maybe because no matter their life-history traits, species are occurring relatively less in human-modified areas. Potential reasons for this absence of effect could also be due to the large size of the cells (5 km²) or the mosaic landscapes of the GRBR, which attenuate or render undetectable certain effects.

It should be noted that the community of species included in this study represents a truncated community compared with the set of species historically present in the GRBR (Baard et al., 2015), that is that the species really vulnerable to humans are probably already extinct in the area. Indeed, the Knysna elephant population is practically extinct (Moolman et al., 2019), while lions (*Panthera leo*), hippopotamus (*Hippopotamus amphibious*) and buffalos (*Syncerus caffer*) no longer occur (Baard et al., 2015). Including information on mammals historically present in the areas could emphasize the effect of life-history traits, such as the body mass, on species occurrence in human-dominated areas. However, our study of mammal species persistence in multifunctional landscapes nevertheless suggests that human-induced modifications could lead to the selection of specific species traits at a local scale, mostly resulting in a change of the community structure in favour of smaller and generalist species, with a fast reproduction strategy. The selection in anthropogenic landscapes of smaller species, or species with more generalist diet has been described in the USA and worldwide (Newbold et al., 2018; Santini et al., 2019; Suraci et al., 2021). Diet and biodemographic traits were good predictors of species persistence and responses to human-dominated landscapes and should help in understanding the conditions for a species to be synanthropic (tolerant of human-modified habitats) rather than anthropophobic, as defined by Hulme-Beaman et al. (2016). Attraction to human-dominated areas and potential associated resources (anthropophilic behaviour) could be linked to species with small body mass and opportunistic diets. We, therefore, suggest further investigation of the link between individual personality traits and the typology defined by Hulme-Beaman et al. (2016). Such work will help managers to develop and implement adequate conservation measures to reduce local biodiversity loss (Carter & Linnell, 2023).

Finally, building single-species occupancy models integrating LEK and CT data was an efficient way of including datasets from different survey protocols to answer a similar ecological question.

Integrating datasets enable researchers and managers to study a larger geographical area, while increasing species detection. Both methods are complementary (Bernard, Guerbois, Venter, et al., 2024). In one hand, people can provide a lot of valuable information, not only on the presence of a species but on the context of an area (Bernard, Fritz, Dufour, et al., 2024), while covering a large geographical area with little effort (financial and technical). In parallel, CTs remain essential in areas where people do not go or to detect very rare and cryptic species, which can strongly avoid human encounters (Bernard, Guerbois, Venter, et al., 2024). Multi-species occupancy modelling approach could have been used to improve the model fit by leveraging information from common species to help inform rare species; however, such models are often more challenging to use than single-species occupancy models. Thus, the proposed approach can be easily used by conservationists and managers to valorize various sources of biodiversity monitoring data and develop systematic ecological monitoring program as well as more social and inclusive approaches, that are complementary to design socially accepted conservation measures (Stern & Humphries, 2022; Volski et al., 2021).

AUTHOR CONTRIBUTIONS

Hervé Fritz, Chloé Guerbois and Alice Bernard conceived the original idea. Lizette Moolman, Melanie A. de Morney and Alice Bernard collected the data. Alice Bernard performed the analyses and led the writing of the manuscript. Hervé Fritz, Chloé Guerbois Jan A. Venter, Lizette Moolman, Melanie A. de Morney and Alice Bernard contributed to the reviewing and editing of the drafts.

ACKNOWLEDGEMENTS

We thank all the respondents of the survey. We would like to thank as well as South African National Parks (SANParks) and CapeNature who approved this research. We are particularly grateful to all SANParks agents who assisted us, as well as people from Nelson Mandela University or the IRL REHABS who helped us with the fieldwork. We are particularly grateful to Jeffrey Doser for his help and recommendations in using the spOccupancy package. We would also like to thank the anonymous reviewers for their insightful comments and suggestions.

FUNDING INFORMATION

This study was funded as part of a grant from the 'IDEX de l'Université de Lyon' and field support from the CNRS (through its Institute INEE) and the Université de Lyon 1, allocated to the International Research Laboratory REHABS.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.41ns1rnph> (Bernard, Guerbois, Moolman, et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Correlation between the variables used in the Principal Component Analysis on the diet of species.

Figure S2. Correlation between the variables used in the Principal Component Analysis on the biodemographic strategy.

Figure S3. Results of the first two axis of the Principal Components Analysis on mammal species diet: the first axis to describe a gradient from a specialist (left) to a generalist (right) diet and the second axis a gradient of herbivory, with carnivores and top and herbivores at the bottom.

Figure S4. Results of the first two axis of the Principal Components Analysis on mammal species biodemographic strategy: the first axis represents a gradient from species with a short (left) to long (right) generation length, the second axis express a trade-off between gestation length and age at sexual maturity.

Figure S5. Results of the first and third axis of the Principal Components Analysis of mammal species biodemographic strategy of the Garden Route.

Figure S6. Distribution of the four variables used in the generalized linear model.

Figure S7. Correlation between the candidate variables used in the generalized linear model.

Table S1. Description of the proportion of type of resources diet as well as various variables describing the traits of each species, extracted from EltonTraits and PanTHERIA database (Jones et al., 2009; Wilman et al., 2014).

Table S2. Proportion of variance explained by each axis and cumulative variance explained for the Principal Components Analysis of mammal species diet.

Table S3. Results of the Principal Components Analysis of mammal species diet.

Table S4. Proportion of variance explained by each axis and cumulative variance explained for the Principal Components Analysis of mammal species biodemographic strategy.

Table S5. Results of the Principal Components Analysis of mammal species biodemographic strategy.

Table S6. Bayesian p -value calculated using Freeman–Tukey statistic test and a Chi-squared test both on the detections and the occupancy models for each data set (CT and survey) to evaluate the fit of each model.

Table S7. Estimates and 95% confidence intervals (CI) for integrated occupancy models testing the effect of anthropogenic variables on species responses.

Table S8. Estimates and 95% confidence intervals (CI) for integrated occupancy models testing the effect of variables on species detection.

Table S9. Estimates, standard error and p -value for the linear regression models testing the effects of species trait values (first two principal components from the trait PCA, see Table S3) on species responses from the estimates of the general linear model.

Appendix S1. Online questionnaire.

Appendix S2. Online questionnaire introduction and consent form.

How to cite this article: Bernard, A., Guerbois, C., Moolman, L., de Morney, M. A., Venter, J. A., & Fritz, H. (2024).

Combining local ecological knowledge with camera traps to assess the link between African mammal life-history traits and their occurrence in anthropogenic landscapes. *Journal of Applied Ecology*, 61, 2470–2482. <https://doi.org/10.1111/1365-2664.14742>