



# Habitat structure, not the anthropogenic context or large predators, shapes occupancy of a generalist mesopredator across protected areas in South Africa

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## Abstract

Black-backed jackals (*Canis mesomelas*) are opportunistic mesopredators occupying a variety of ecosystems across South Africa (SA). They can move between protected areas (PAs) and surrounding human-dominated landscapes where they are prone to conflict with wildlife and livestock farmers and subsequently face high persecution rates. However, it remains unclear to what extent the anthropogenic landscape matrix in which PAs are embedded affects black-backed jackal occupancy within PAs at large spatial scales. Therefore, in this study, we explore how different sources of environmental variation inside and outside PAs influence the patterns of jackal's occupancy within PAs. We used 309 camera traps across 15 PAs in SA to respond to the following questions: (i) How does the landscape matrix surrounding PAs affect black-backed jackal occupancy compared to the landscape characteristics inside PAs? (ii) How does the presence of large carnivores affect black-backed jackal occupancy under these varying conditions of anthropogenic and PA landscape characteristics? When contrasting the effect of landscape variables and large predators at different spatial scales (fine-scale at site vs coarse-scale at reserve level), we found overwhelming support for tree cover at the camera site level as the main factor driving jackal occupancy with a higher occupancy in open areas. Our results suggest that neither anthropogenic context around PAs nor large predators influence the geographic variation in jackal's occupancy at large scales and that fine-scale habitat attributes are more important. Our study sheds light on the role of bottom-up over top-down mechanisms in driving jackals' distribution, confirming the ecological plasticity of this species to occupy different environments and suggesting that management of this species must be planned at local scales.

**Keywords** Anthropogenic landscapes · Camera traps · Habitat use · Black-backed jackal · Bottom-up · Top-down

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## Introduction

It is well known that human activities such as agriculture or urbanization lead to habitat loss and fragmentation, which have become one of the main causes of the current biodiversity crisis (Díaz et al. 2019; Fahrig 2003; Laurance et al. 2014). In this sense, protected areas (PAs) are pivotal for biodiversity conservation, but even in these areas processes occurring outside their limits can also affect biodiversity and ecosystem function inside the PAs (Defries et al. 2010; Laurance 2012; Woodroffe 1998). Rovero et al. (2019), for example, found that high human population density around protected areas tend to reduce carnivore species richness at multiple PAs worldwide. Human activities surrounding PAs create edge effects that can affect species in different ways, including, for example, limiting mobility or dispersion of species across the landscape, reducing species

richness, abundances, and gene flow (e.g., Correa Ayram et al. 2015; Gibson et al. 2011; Wearn et al. 2016). However, the intensity of the effects of land-use changes on native fauna depends on the structure of these landscapes, such as types of land uses, configuration, human presence, and the potential availability of new resources (Cosentino et al., 2011; Franklin and Lindenmayer 2009; Prugh et al. 2008). Some agroecosystems, for example, can facilitate the occurrence of generalist species (Daily et al. 2003; Muhly et al. 2013; Pardo et al. 2019), while others may act as barriers or “ecological traps” with an elevated risk of mortality of rare and specialized species (e.g., Battin 2004; Minnie et al. 2018; Van Der Meer et al. 2014).

The rate of mortality in PA borders can be high for many carnivore species (Woodroffe 1998). For example, the population of leopards (*Panthera pardus*) in the Phinda-Mkhuze Complex (PMC), South Africa, was found to be lower at the borders and outside the PAs than closer to core areas due to high mortality rates outside the reserve (Balme et al. 2010). However, other species may benefit from edge habitats (Fleschutz et al. 2016). Black-backed jackals (*Canis mesomelas*), for example, are considered a problematic species in farmlands or game (wildlife) ranches where they are persecuted and killed in retaliation for preying on domestic livestock and commercially valuable wildlife (Bagniewska and Kamler 2013; Blaum et al. 2009; Thorn et al. 2013). Despite this persecution, population seems to remain stable in some areas (Minnie et al. 2018, 2016), while in others, population of jackals can be negatively affected by crops (Ramesh and Downs 2015). South African protected areas, as most PAs worldwide, are embedded in a matrix of different anthropogenic uses. However, there is little information about how processes occurring outside these PAs could also influence populations or the distribution of jackals at large scales inside the PAs. Since most of the PAs in South Africa are fenced, it is likely that the effects of surrounding landscapes and edge effects are minimized, but there is still a paucity of information in this regard. Smaller species, including mesopredators such as black-backed jackal, typically are not limited by fences and therefore this species can move across anthropogenic landscapes surrounding the PAs (Kaunda 2001; Minnie et al. 2018, 2016).

The effect of anthropogenic factors on species dynamics can also be influenced by bottom-up and top-down processes. These two processes are important in regulating the structure, distribution, and relationships among mammalian assemblages (e.g., Elmhagen and Rushton 2007; Laundré et al. 2014). The bottom-up process includes factors at lower levels of the trophic web that influence upper levels, such as forage or food resources availability, habitats, prey abundance, among others (e.g., Macdonald 1983). On the other hand, top-down refers to the effect of top predators over lower trophic levels (Laundré et al. 2014). This top-down

“control” or suppression mechanism can occur directly via, for example, predation and killing or by indirect competition, including what has been called “landscape of fear” (Laundré et al. 2014, 2001; Prugh and Sivy 2020). In some systems, bottom-up forces such as prey availability or prey size have proven to be more important than top-down forces for determining species occupancy and biomass fluxes (e.g., Santos et al. 2019, Owen-Smith and Mills, 2008, respectively). However, these two mechanisms do not necessarily act in isolation and bottom-up, and top-down factors exert simultaneous effects (Jachowski et al. 2020; Prugh and Sivy 2020). Whether top predators are more important than landscape or habitat characteristics on mesopredator distribution in fenced PAs embedded in human dominated matrix in South Africa remains little explored (e.g., Gigliotti et al. 2020).

Recent evidence also suggests that top predators’ effect over other carnivores is context dependent, and the direction of the effect is not always negative (Gigliotti et al. 2020; Prugh and Sivy 2020; Swanson et al. 2016). For example, a facilitation process may occur when mesopredators can access carcasses left by large predators’ kills (Prugh and Sivy 2020). On the other hand, species responses also vary according to the geographical scales, as demonstrated by Sivy et al. (2017) who found a negative response of most mesopredator species to gray wolf (*Canis lupus*) abundance at the landscape or large scale, but a positive association at smaller or local scales (i.e., within a study area). Therefore, understanding how mesopredator species interact with other carnivores and the environment is essential to inform management decisions, especially in countries such as South Africa where much of the management of protected areas (private and public) is focused on large carnivores and ecotourism.

The black-backed jackal, hereafter referred to as jackal, is a medium-sized generalist mesopredator (5–15 kg) (Minnie et al. 2016). It is the most widespread species of carnivore in the semi-arid regions of southern Africa (Macdonald et al. 2004), occupying a variety of habitats but preferring open woodlands and often avoiding floodplains and grasslands (Kaunda 2001; Macdonald et al. 2004). Despite being a common species, few investigations have assessed their spatial relationship with top predators and other mesopredators (Kamler et al. 2020b). However, it is known that suppression (Curveira-Santos et al. 2021) and facilitation (Hayward et al. 2017) mechanisms can take place. For example, lions (*Panthera leo*), African wild dogs (*Lycaon pictus*), and other large carnivores kill jackals (Kamler et al. 2020a). It is known that the density of jackal populations varies considerably depending on the area, farm management, and density and composition of large carnivore community (Minnie et al. 2016). Similarly, protected areas are often seen as refugia for jackals which can act as sources to replenish persecuted populations through compensatory

immigration (Minnie et al. 2018). These ecological characteristics of jackals make them an interesting model species to compare potential human-driven forces outside the reserve and contrast these characteristics with conditions inside.

Here, we used a large-scale camera trap dataset across 15 South African PAs to investigate how the geographical context around and inside the PAs influence jackal occupancy within PAs. Specifically, we explore the relative influence of habitat conditions within each PA as a proxy for bottom-up processes (i.e., tree cover), the presence of top predators, PAs features such as size and age, and anthropogenic factors in the reserve's surroundings. In addition, to understand the scale of jackal's responses, we contrast the effect of the above variables at fine scale (specific to each camera station) and variables measured at the reserve-scale (common to all cameras in a reserve). This way, we gathered insights on how the distribution of jackals is driven by fine-scale responses to continuous environmental gradients, irrespective of the reserve context, and how changes in occupancy rates (i.e., the proportion of occupied/used area) across PAs may be influenced by the reserve context or presence of large predators.

Since jackals can move inside and outside PAs interchangeably (Kaunda 2001), we hypothesized that factors that characterize the anthropogenic landscape around the PAs could play an essential role in jackal occupancy inside PAs. As such, we predicted that the effect of anthropogenic features outside the reserve can have a positive or negative effect on jackal's reserve level occupancy due to its natural history. If jackals tend to use anthropogenic areas for foraging, we expect this species to be more common in PAs surrounded by more anthropogenic features such as livestock, agriculture, or human infrastructure, assuming they use these areas for foraging. Therefore, the occupancy of jackals inside the PAs would be higher in PAs surrounding by higher levels of anthropogenic activities ( $\beta > 0$ ). It is also possible that jackals are in conflict with people surrounding the reserve; thus, we would expect high retaliatory killing and therefore this might affect local jackal abundances (Blaum et al. 2009), which might impact population inside the PAs. Therefore, this lethal management could reduce their occurrences ( $\beta < 0$ ). Additionally, we assessed the effect of presence of lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*), and leopards (*Panthera pardus*) on jackal's occupancy at both scales. Based on the suppression mechanism, we predict that all these predators will have an important negative effect on jackal occupancy at both levels.

## Materials and methods

### Study area

We conducted this study across 15 PAs in South Africa encompassing six biomes (i.e., Fynbos, Grassland, Nama

Karoo, Savanna, Succulent Karoo, and Thicket (Mucina and Rutherford, 2006). PAs included mostly national parks and to a lesser extent private or communal-owned natural and game PAs with varying creation dates and sizes ranging from 93.46 (e.g., Blouberg Nature Reserve) to 19,485 km<sup>2</sup> (e.g., Kruger National Park), and were in altitude ranges between 50 and 1600 m.a.s.l (see S1 for details).

### Data collection and survey design

This research was part of an ongoing camera trap monitoring project called Snapshot Safari South Africa (hereafter Snapshot) which contains multiple surveys across several PAs (Pardo et al. 2021). We filtered the available data to those surveys conducted between 2018 and 2019 considering only a single survey of approximately 3 months per reserve to approximate the closure population assumption of occupancy models (MacKenzie et al. 2002 see below). As per Snapshot protocols, in each reserve, we deployed 16 to 39 (mean: 21) camera trap stations at regularly spaced cells of 5 km<sup>2</sup> (~ 2.3 km apart) for a total of 309 cameras deployed across the country. Although the Snapshot design is not targeting jackals or carnivores only, but the entire mammal community, its spacing is similar to widely recommended standards for camera trap studies on mammal communities (e.g., Ahumada et al. 2011). This distance helps to ensure independence of sampling units (i.e., camera traps) of jackals and other species (see the "Occupancy modeling" section).

Cameras were fixed to trees or metal poles facing animal trails or any evidence of mammal presence, without the use of bait or any attractants. We avoided trails with high human use such as main or secondary roads. Due to the limited number of cameras, not all PAs were surveyed at the same time and therefore some of the sampling periods did not coincide between PAs (see S1 for details of the survey). However, to account for this temporal grouping, we use season as a random factor (see the "Occupancy modeling" section). Each camera was programmed to take three images (one event) with a 1-min time-lapse between events. Most cameras were Cuddeback® black and white flash (Cuddeback, WI, USA) and few were Scoutguard® SG565 incandescent cameras. Images were classified with the help of citizen scientists through the Zooniverse platform (Zooniverse.org, Pardo et al. 2021; Willi et al. 2019), except for three sites (Goegap Nature Reserve, Augrabies Falls National Park, and Khamab Kalahari Game Reserve). These images were tagged manually by a lab technician using Digikam ([www.digikam.org](http://www.digikam.org)), an open-source digital photo management application, and CamtrapR (Niedballa et al. 2016), an R package designed to analyze camera trap data.

## Covariates

Since we were interested in understanding the effect of landscape features outside (i.e., the surrounding context) and inside the PAs, we grouped variables according to these two contexts. Features inside the PAs were related to (a) habitat conditions that could serve as proxies for potential bottom-up processes (Macdonald 1983), and (b) potential top-down forcing (i.e., presence of large predators)—see details below. Since the responses of animal communities can be influenced by the scale at which features are measured (e.g., Prugh and Sivy 2020), we set the following contrast. For variables inside the PAs, we contrasted the effect of fine-scale variables (specific to each camera station) to variables measured at the reserve scale (common to all cameras in a reserve such as reserve age or area) and to proxies of human disturbances in the reserve's surroundings (e.g., human population density and anthropogenic land uses; Table 1). All variables surrounding the PAs were assumed to act only at the reserve scale, due to the lack of cameras outside the PAs to contrast fine-scale variables.

## Variables surrounding the protected areas

Given that jackals move across reserve fences, we used variables that characterize the anthropogenic landscape around the PAs to test the influence of the surrounding context on jackal occupancy inside the PAs. These variables included the spatial extent (area) of land use type (i.e., agricultural, built-up, conservation, other wildlife PAs) bordering the PA (see Table 1). To extract the variables of the context surrounding the PAs, we created a buffer of 2 and 5 km around the PAs and characterized each feature within this space using ArcGis® software (ESRI, 380 New York Street, Redlands, CA 92,373, USA). We used this arbitrary distance based on jackals home range which can vary between ~10 and 16 km (Kamler et al. 2019; Kaunda 2001). We contrasted these two scales using Spearman's rank correlation coefficient and found both measurements correlated (> 0.90). Therefore, we decided to use only those values at 2 km buffer because the gradient of the values for most variables was better. In addition, the 2-km scale is roughly the radius of the abovementioned home ranges. We used the 2013–2014 National Land-Cover Dataset which is based on 30 × 30 m raster cells (GeoterraImage 2015) to extract landscape features surrounding the PAs. The value of the areas was estimated using the “tabulate area” function in ArcGis based on the processing cell size and multiplied the value by 1000 so numbers are easier to interpret. For the area of agriculture, we grouped these classes: Commercial Annuals (rainfed), Commercial Pivot, Commercial Permanent (Orchards/Vines), Subsistence, Sugarcane pivot, Sugarcane non-pivot, as per GeoterraImage classification (2015).

Classes for build-up included Mine, Bare, Semi-bare, Mine water seasonal, Mine water permanent, Mine Buildings, Commercial, Industrial, Informal, Residential, Schools and Sports Grounds, Schools and Sports Grounds, Smallholding, Sports and Golf, and Township and Village (GeoterraImage 2015).

For the human density measure, we used 2015 World-Pop estimate for the number of people per 100 m grid square (<https://africaopendata.org/dataset/south-africa-population-density-2015>). To calculate the size of protected areas (in km<sup>2</sup>), we used spatial files from the South African Protected Areas Database (SAPAD, <https://egis.environment.gov.za/>) and shape files provided by the PAs when available, which were more up to date. In the case of large parks such as Kruger (~19,400 km<sup>2</sup>) and Kgalagadi (~38,000 km<sup>2</sup>), the area covered by the camera grids was not proportional to their size to make inferences for the whole reserve and therefore we did not consider the full extent of these parks for the area calculation. To compensate for this, the area of these parks was assumed to be the minimum convex polygon using the outermost cameras of the grid. This helped to avoid extreme outliers that could bias the analysis and therefore improved the modeling without affecting the inferences as the final polygon used to calculate the area for these parks still represented larger areas in the dataset.

## Variables inside protected areas

We selected two landscape variables that act at the site level and therefore vary per camera site, percentage of tree cover (*tree.cover.site*) and distance to the border of the reserve (*dist.border*) as a proxy for potential edge effects. It is likely that the importance of edge effects captured by a *dist.border* depends on the degree of anthropogenic pressure outside PAs. Therefore, by exploring both metrics, we aimed to capture this potential relationship. We also included three variables acting at the reserve scale: tree cover (*tree.cover.res*) for which we used the average value of all cameras within the reserve, area of the reserve in km<sup>2</sup> (*area.res*), and establishment year (*year*). The tree cover was extracted from MODIS vegetation continuous fields dataset at a 250-m resolution (<https://modis.gsfc.nasa.gov/data/datap>) as a proxy for vegetation structure. For this, we used a 1000-m-radius buffer around the cameras. We determined this radius after contrasting with measures at 100 and 500 m radius using Spearman's correlation coefficient which suggested that the three measures were correlated (Spearman's coef. > 70). We also accounted for the presence of three large predators (lion, leopard, spotted hyena) at both scales as well as its richness (total number of large carnivores present in the reserves), since mortality of mesopredators can be three times higher in systems with three large predators compared to those systems with only one large predator (Prugh and

**Table 1** Site and reserve covariates used to estimate jackal occupancy ( $\Psi$ ) across different protected areas in South Africa and expected relationships. For complete description and source of data, see text

Scale of the variable	$\Psi$ variables	Code (unit)	Prediction/rationale
Site-scale variables (camera site)	Percentage of tree cover around camera trap	<i>tree.cover.site</i> (%)	Jackals prefer open woodland areas (Macdonald et al. 2004); therefore, we expect that occupancy of jackal will decrease as the tree covers increase ( $B1 < 0$ )
	Distance to the border of reserve	<i>dist.border</i> (km)	If jackals prefer to hunt and roam in other land uses bordering the PAs, we expect that occupancy of jackal would be higher at sites close to fences ( $B1 < 0$ ) (Kamler et al. 2019). However, if killing of jackals is frequent next to PAs, we expect the opposite relationship, with more detections towards the center of the reserve (see Balme et al. 2010)
	Presence of large predators (lions, leopards, spotted hyenas)	<i>lion.site</i> , <i>leopard.site</i> , <i>hyena.site</i> (1–0)	If large predators exert an important negative control over jackals (suppression, Curveira-Santos et al. 2021), the occupancy of jackal would decrease when predators are present at the sites ( $B1 < 0$ ). However, this effect can be neutral or even positive under the facilitation hypothesis (Fourie et al. 2015)
	Large predator species richness	<i>pred.rich.site</i>	If large predators exert a negative effect over mesopredators, we expect jackal's occupancy to decrease when sites have more than one predator species ( $B1 < 0$ ) (see Prugh and Sivy 2020)
Variables at reserve level inside and around the PAs	Average percentage of tree cover inside the reserve	<i>tree.cover.res</i> (%)	Jackals prefer open woodland areas (Macdonald et al. 2004); therefore, we expect that occupancy of jackal will decrease as the tree covers increase ( $B1 < 0$ )
	Reserve size	<i>area.res</i> (km <sup>2</sup> )	Bigger PAs would have higher jackal occupancy ( $B > 0$ ) assuming a positive relationship between abundance and area and the potential of larger PAs to buffer edge effects (Woodroffe 1998). However, bigger areas could also reduce the detection probability of the species as more area is available for the species to use
	Reserve age	<i>year</i>	Assuming that the date of declaration of a PA implies improvement in conservation and restoration processes, we expect that older PAs will have higher jackal occupancy ( $B > 0$ )
	Presence of predators (lions, leopards, spotted hyenas)	<i>lion.res</i> , <i>leopard.res</i> , <i>hyena.res</i> (1–0)	If top predators exert an important negative control over mesopredators, we expect jackal occupancy to decrease when PAs are also occupied by these species ( $B1 < 0$ )
	Large predator species richness	<i>pred.rich.res</i>	If large predators exert an important control over mesopredators (Prugh and Sivy 2020), we expect jackal occupancy to decrease when PAs have more than one species of predators ( $B1 < 0$ )
	Context of land use around the PAs (within the 2 km buffer from reserve edge); human population density, proportion of agriculture, build-up (infrastructure), area other protected areas	<i>human_agri_build.up_area.PA</i> (tabulated area)	If jackals tend to occur in anthropogenic landscapes and use PAs as a refuge, the occupancy probability will be higher in PAs surrounded by more anthropogenic influence ( $B > 0$ ). However, if jackal is being killed outside, then it can negatively affect occupancy inside the PAs ( $B < 0$ )

Sivy 2020). Given that one of the 15 reserves has a separate area with lions and another one without lions, we considered this reserve as two separate reserves for analysis (TSL with lions, and TSK with no lions).

## Occupancy modeling

To estimate the influence of the variables on jackal occupancy across PAs, we followed a single season likelihood-based occupancy model (MacKenzie et al. 2002). Occupancy ( $\psi$  or  $psi$ ) can be defined as the proportion of an area occupied by a species or the probability of occurrence at a spatial survey unit (camera site in our case). The advantage of the occupancy framework is that it explicitly accounts for two important parameters, the detection probability if the animal is present ( $p$ , related to the observational process) and occupancy, which is the ecological parameter of interest in this study (MacKenzie et al. 2002). This modeling approach is based on detection/not detection data at each site along temporal replicates (occasions). We, therefore, constructed detection histories compiling the photographs into 11 survey occasions formed by the combination of 8 consecutive days (i.e., one occasion) and performed all analyses in the R package Unmarked (Fiske and Chandler 2011). We created the detection history and the camera operation matrix using *CamtrapR* package (Niedballa et al. 2016). Stacking the detection history into days helps to reduce potential temporal autocorrelation and better accommodate zero-inflated data common in these studies.

Since not all cameras operated for the entire survey period, we used the last photo recorded as the end of the survey to account for differences in the effort per site. This is accounted in the detection history by including NA for occasions at which cameras did not operate, without affecting the occupancy modeling (see MacKenzie et al. 2018). Jackal's home range can vary around 9 km<sup>2</sup> (Kamler et al. 2019); therefore, there is a probability that the same individual moves across camera sites, violating the closure assumption or independence between sites; consequently, here we interpret site occupancy in terms of habitat use (MacKenzie et al. 2018). Before building the models, we conducted an exploratory data analysis to identify outliers and collinearity between variables as suggested by Zuur et al. (2010). All variables were standardized to  $z$  value prior to model implementation, and subsequent analyses and visualizations were performed in R (R Development Core Team 2014).

We used three variables to account for detection probability: tree cover at camera site scale, camera days, and type of flash of the camera used (flash; black vs white). We expected that tree cover could affect detection probability as the density of the vegetation can block the field of view of the camera and affect the sensitivity of the lens to trigger the camera, hence affecting the operation of the camera and

the detection probability when the animal is present. Dense vegetation can also affect the quality of photos hindering the correct identification of the species and could influence species to walk through more open nearby areas. Similarly, the number of days the camera is active also affects detection probability as cameras active for longer periods will have more chances to detect a species when present. Flash type could also disturb species affecting the detectability and identification of species due to overexposure of images, especially in white flash cameras with animals passing too close from the cameras (Wearn and Glover-Kapfer 2017).

To understand the importance of the covariates in determining jackal's occupancy, we used a model selection approach based on Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002). We considered models with  $\Delta AIC < 2$  as the top candidate set with substantial evidence as competing models, and used model AIC weight (AICw) to determine the strength of support for each models (i.e., we considered covariates to be important if they had relatively high-summed Akaike weights and they outcompeted the null model [ $p(\cdot), \psi(\cdot)$ ]) (Burnham and Anderson 2002). Since surveys were conducted at different times of the year, we included this potential source of variation between surveys (and potential correlation of sites within each season) by including these periods related to seasonality as a random effect in all models (a category of 8 seasons that specifically accounted for the sampling periods, see S1).

Since we were more interested in the effect of the above factors and the scale of this effect, we did not consider different additive models (i.e., multiple variables in the same model). However, to understand whether the anthropogenic context surrounding the reserve had a more important effect (all together) over internal features, we built three additive models, one adding all anthropogenic features outside the PAs (i.e.,  $global.out = human + agri + build-up$ ), another including all features at the reserve level inside the reserve ( $global.in.res = area.res + year$ ), and all features inside the PAs at the camera site level ( $global.in.site = tree.cover.site + dist.border$ ) (see S2 for all models). We considered there was no sufficient knowledge to favor a particular combination of factors over others, and we preferred not to contrast too many models to improve inferences as recommended by Morin et al. (2020).

For the model ranking, we first selected the best models for  $\Psi$  while using a general model for  $p$  (all variables for  $p$ ) as recommended by MacKenzie et al. (2018). Including the above additive models, we built 22 a priori models for  $\Psi$  (S2) which were ranked as described in the previous paragraph. In a second stage, we used the best models for  $\Psi$  and conducted a second model selection for  $p$ , using all possible combinations of  $p$  and  $\Psi$ . We accounted for model fit by using 10,000 parametric bootstraps (MacKenzie and Bailey

2004) with the `mb.gof.test` function from package `AICcmodavg` (Mazerolle 2020). Models with  $c\text{-hat} \sim 1$  were considered adequate descriptors of the data whereas  $c\text{-hat} > 1$  were considered over dispersed. If the most complex model was found to be overdispersed, we included the  $c\text{-hat}$  value in the model selection and used the quasi-corrected AICc (QAICc) instead.

## Results

After the exploratory analysis, we selected 291 sites from the initial 309 to run the analysis totaling an effort of 20,523 camera days (S1). Only tree cover at the site level was collinear with tree cover at the reserve level. However, since we were not using both variables together in any model and we were interested in looking at potential scale differences in response, we kept both variables. The most complex model (*global.out*) was found to be slightly over dispersed ( $c\text{-hat} = 1.34$ ); therefore, we used the quasi-corrected AICc (QAICc) in the model selection.

Jackals occurred in most of the studied PAs with detections in 13 out of the 15 PAs and 93 out of 291 surveyed camera sites (0.32 naïve occupancy). Sum of detections, however, varied between 4 and 30 at each reserve, with sites such as Camdeboo NP and Kgalagadi Transfrontier Park presenting the most detections and Blouberg Nature Reserve and Augrabies Falls NP the least (S3). Only two models were selected as the most plausible explanations in the occupancy ( $\Psi$ ) models (i.e., maintaining the general model for detection probability– $p$ ) with tree cover at the site level showing the most support ( $\omega_i = 56\%$ ) followed by the global model at the site level inside the PAs (*tree.cover.site + dist.border*) ( $\omega_i = 22\%$ ) (Table 2, S2). After selecting for the best models of  $p$ , we found four final supported models. Flash type and effort (*cam.days*) were the most important factors influencing the detection probability of jackal; however, the model including constant detection was also included in the four most parsimonious models, suggesting that jackal detection probability is not strongly influenced by the factors included in this analysis (Table 2).

The final model ranking suggests that tree cover at the camera site level was the most important driver of jackal occupancy appearing in the four most supported models totaling an AICc weight ( $\sum \omega_i$ ) of 76%. On the other hand, the global model inside the PAs (*global.in.site*) had a lower support with  $\omega_i = 12\%$  (Table 2). These results suggest that the presence of top predators was not an important driver of jackal occupancy which was clearly determined by a habitat factor at the site level. Furthermore, this also suggests that the responses of jackals to landscape variables are stronger at the site scale as opposed to any characteristics at the reserve scale. The untransformed coefficients

of the best model [ $p(\text{flash})$ ,  $\Psi(\text{tree.cover.site})$ ] show that tree cover at the site level had a negative effect ( $\beta = -1.158$  (SE 0.428)) (Fig. 1). Although the third best model includes tree cover and distance to border in  $\Psi$ , the latter had a very low coefficient, and CI overlapped zero suggesting its effect is negligible [ $\text{tree.cover.site} = -1.1522$  (SE 0.419) vs  $\text{dist.border} = -0.0967$  (SE 0.161)]. Based on the best model, the average estimated occupancy using all sites across PAs was 0.40 (min = 0.0017, max = 0.75916, SD = 0.1680576). In Fig. 2, we show the predicted estimated occupancy across the country with emphasis on predictions inside PAs (see also S4). Only 6 of the 15 PAs had an average probability of occupancy greater than 0.5 (3 in Savanna biome: Khamab Kalahari Game Reserve, Kgalagadi Transfrontier Park, and Pilansberg National Park; one Nama Karoo and Thicket biome: Candeboo National Park; one Nama Karoo biome: Karroo National Park; and one containing Nama Karoo and Grassland biomes: Mountain Zebra National Park (Fig. 3)); all of which have large predators except for Candeboo NP. Although there was great variation on occupancy across PAs (Fig. 3), this variability was not explained by any of the reserve scale variable and mostly depended on gradients of tree cover at the site level.

## Discussion

Here, we analyzed jackals' occupancy patterns in South Africa to elucidate how anthropogenic landscapes around PAs affect jackal occupancy inside the PAs compared to features within them. We found overwhelming support that tree cover at the site level was the main driver of jackal occupancy over any of the other variables explored. This confirms that it is more likely to find jackals using areas with more open habitats, as shown by Kaunda (2001) and Loveridge and Macdonald (2003). On the other hand, the fact that none of the other variables characterizing environmental conditions inside and outside the PAs, at different spatial scales (site or reserve level), had clear influence on jackal occupancy supports the common notion that jackals exhibit high ecological plasticity and are thus tolerant to various degrees of anthropogenic disturbance (Hayward et al. 2017; Loveridge and Macdonald 2003). For example, a radio-tracked subadult male moved over long distances across the Central Karoo crossing 110 farms and covering over 2000 km in 4 months (Nattrass et al. 2019). Another study found that locations outside a reserve in Zimbabwe accounted for 21% of the records (Kaunda 2001). Furthermore, jackals are also opportunistic predators that can adapt to available resources and shift diet preferences (e.g., Fourie et al. 2015). Our study adds evidence that anthropogenic features are not important drivers of jackal distribution.

**Table 2** Model selection results of the influence of landscape factors and large carnivore presence on black-backed jackal (*Canis mesomelas*) occupancy across South Africa. Only models with delta AICc < 2 are shown (for the complete set of models, see supplementary material S2)

Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
Model selection for occupancy ( $\Psi$ )							
$p(\text{Flash} + \text{Cam.Days} + \text{tree.cover.site}), \Psi(\text{tree.cov.site})$	7	1098.252	0	1	0.568	-541.928	0.568
$p(\text{Flash} + \text{Cam.Days} + \text{tree.cover.site}), \Psi(\text{global.in.site})$	8	1100.153	1.901	0.386	0.219	-541.821	0.787
Model selection for detection probability ( $p$ ) based on above							
$p(\text{Flash}), \Psi(\text{tree.cover.site})$	5	1096.395	0	1	0.302	-543.092	0.302
$p(\cdot), \Psi(\text{tree.cover.site})$	4	1097.232	0.837	0.658	0.199	-544.546	0.502
$p(\text{Flash}), \Psi(\text{global.in.site})$	6	1098.119	1.724	0.422	0.128	-542.911	0.629
$p(\text{Cam.Days}), \Psi(\text{tree.cover.site})$	5	1098.122	1.727	0.422	0.127	-543.956	0.757

K, number of parameters in the model (season is included in all models as a random factor to account for this potential confounding factor); *Delta\_AICc*, difference in AIC values between each model with the lowest AIC mode (best model); *ModelLik*, model likelihood; *AICcWt*, Akaike weight; *Cum.Wt*, cumulative Akaike weight; *LL*, log-likelihood. For model description, see text and supplementary material for all a priori models. *tree.cover.site* = percentage of trees at site level, *global.in.site* = *tree.cover.site* + *distance to border*

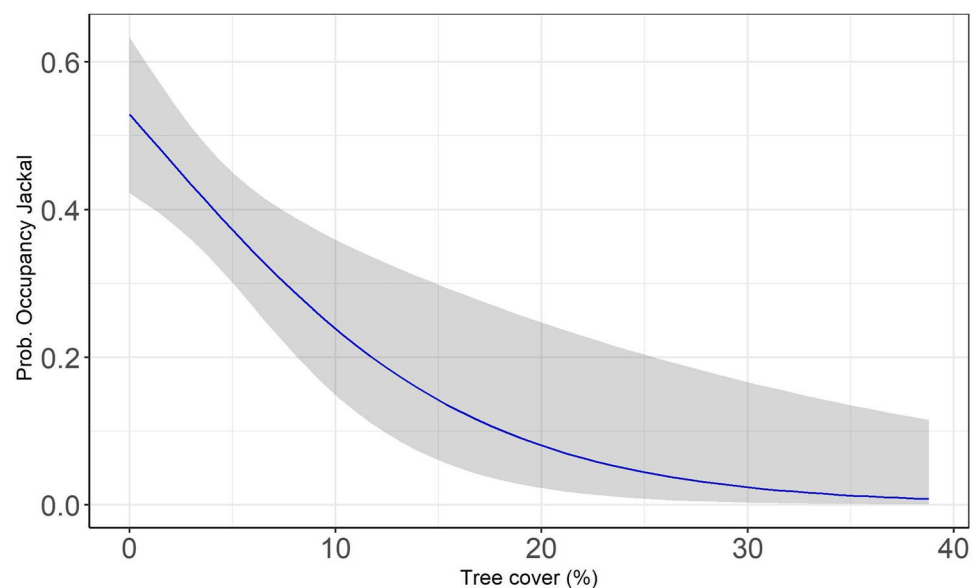
Jackals were more likely to occur in open habitats (at fine scale) across their range, which seems to match the greater occupancy in these biomes observable from raw data (e.g., dry habitats such as Nama karoo, Fig. 3). As such, and assuming a positive relationship between abundance and occupancy (MacKenzie and Nichols 2004; Steenweg et al. 2018), our results suggest that jackal is more common in PAs dominated by Savanna and Nama Karoo biomes, and much less common in Fynbos. Interestingly, despite the differences in occupancy across PAs, this variability was not explained by any of the reserve scale variables such as area, tree cover, or presence of predator at the reserve level as it mainly depended on tree cover at fine scales (camera site). This suggests that responses of jackals inside depend on processes related to fine-scale habitat structure, irrespective of the PA context (within and surrounding) or other potential

variables that were not included in this analysis (e.g., habitat mediated variation in food availability).

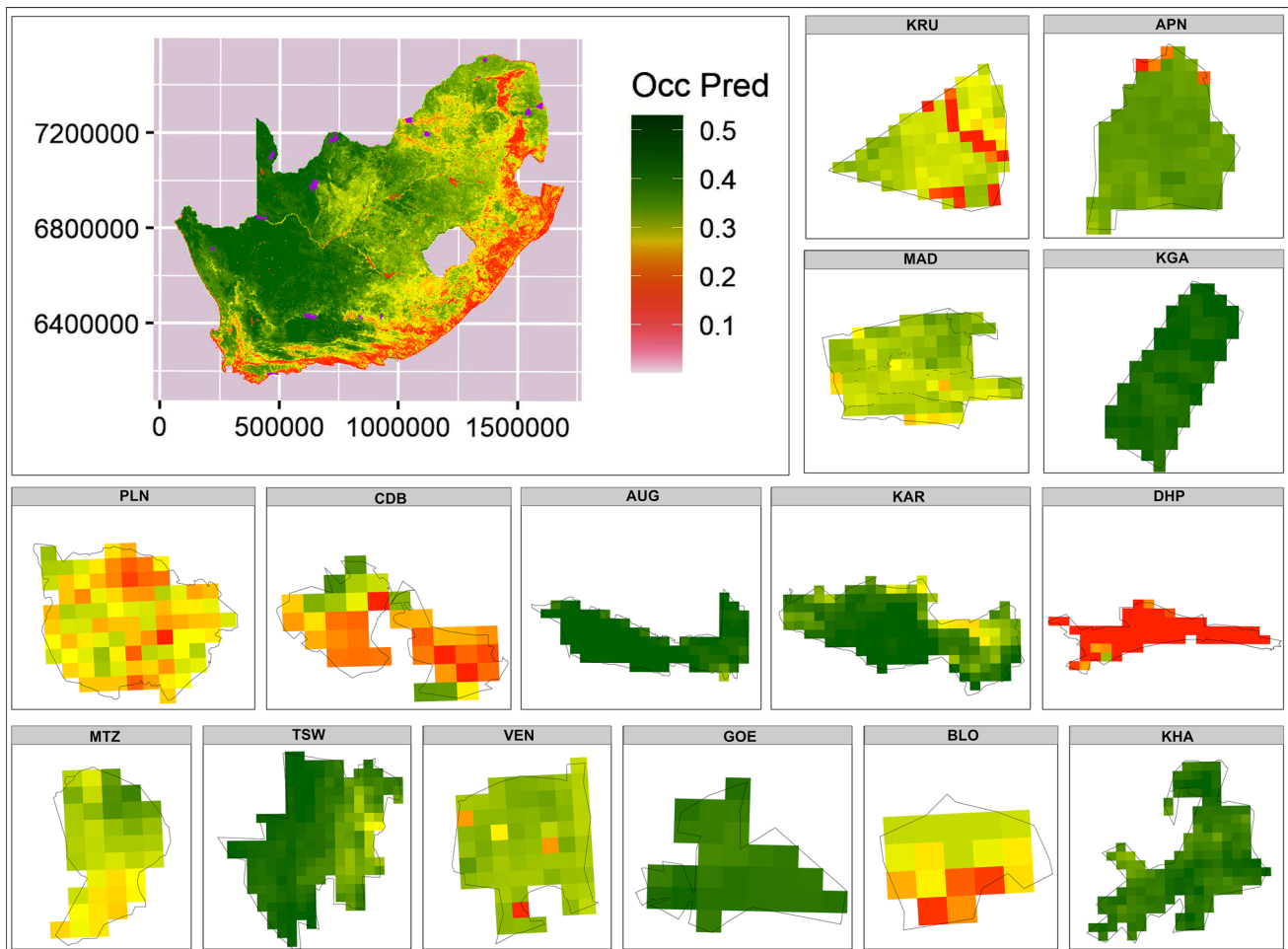
### Predictions about large predators

Although large predators have been shown to exert an important influence in the behavior of other large- and medium-size predators (Prugh and Sivy 2020), our results showed that habitat characteristics are more important for jackal's occupancy than the presence or richness of apex predators at any scale, contrary to our predictions. The lack of evidence for a top-down control has been proved in other canids (mesopredators). For example, in Australia, Castle et al. (2021) demonstrated that removal of dingoes did not increase the abundances of red foxes (*Vulpes vulpes*) or feral cats (*Felis catus*). Similarly, Comley et al. (2020)

**Fig. 1** Effect of tree cover on black-backed jackal (*Canis mesomelas*) occupancy across 15 PAs in South Africa. This plot is based on the best model including  $p(\text{flash}), \Psi(\text{tree.cover.site})$  (categorical variable “season” not included as random effect to improve visualization)







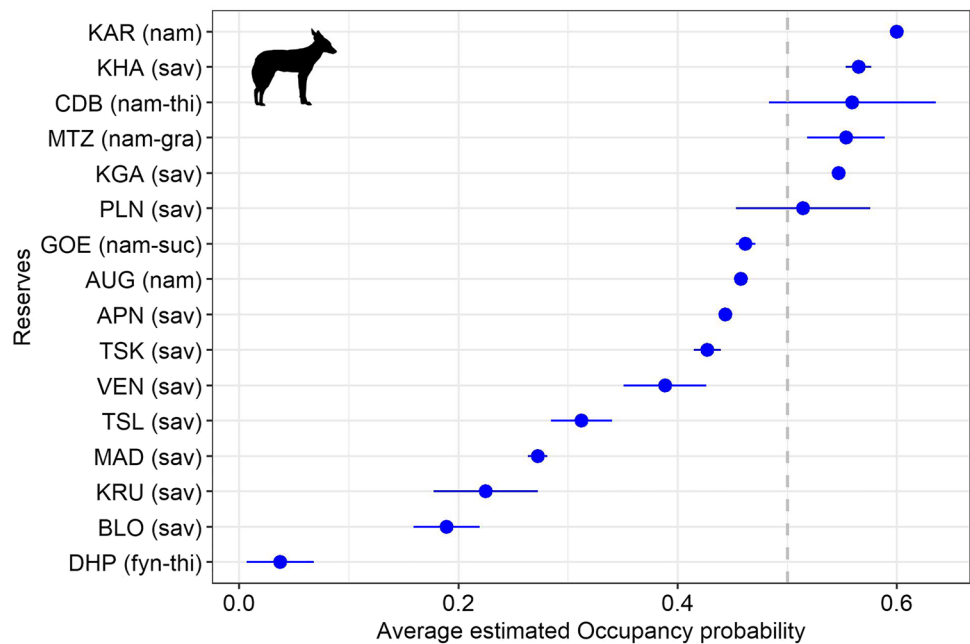
**Fig. 2** Predicted occupancy of black-backed jackal (*Canis mesomelas*) based on top model ( $[p(\text{flash}), \Psi(\text{tree.cover.site})]$ ). Purple in the country map represents the location of the protected areas (for reserves code see S1). The shape and size of Kgalagadi Transfront found that large carnivores did not exert an important influence on black-backed jackals' occupancy ( $\psi$ ) inside a single fenced reserve in South Africa (as in this study), as it was mostly determined by distance to water. However, they also found that lions' and spotted hyaenas' relative abundance negatively influenced the detection probability ( $p$ ) of jackals (while leopards had a positive effect), and that only lions influenced jackals' colonization ( $\gamma$ , under a multi-season occupancy framework) with a negative effect. This lack of effect of large carnivores can be related to other types of fine-scale mechanisms that permit sympatric species to co-occupy rather than dominate functional niches (e.g., temporal and spatial segregation; Karanth et al. 2017), which should be addressed with further research.

If we looked at the effect of large predators in isolation (accounting only for that variable regardless of the model selection), our results suggest that the presence of each apex predator and their richness have a different effect depending on the scale. At the reserve level (large scale), all top

tier Park and Kruger National Park do not represent the full extension of these parks (see "Materials and methods"). TSW is a single reserve with a fenced area for lions (TSL) and another area with no lions (TSK)

predators had a negative influence on jackal occupancy (as predicted). However, at the site level (fine scale), the effect varied, with negative responses for spotted hyena and carnivore richness, but positive for lion and leopard. This demonstrates that the influence of top predators can depend on the scale, similar to what Sivy et al. (2017) found for the gray wolf. Curveira-Santos et al. (2021) also contrasted multiple PAs and found that occupancy rates of mesopredators (including black-backed jackal) in PAs with lions were lower than in areas without lions. Similarly, Yarnell et al. (2013) also found that black-backed jackal density was higher in an area without apex predators lions and wild dog (*Lycan pictus*). Contrary to the above evidence and our study, Kamler et al. (2020b) demonstrated that jackals exhibited spatial partitioning with African wild dogs and lions at fine scale, but not at broad scales within a fenced reserve in South Africa. The above evidence and our study, therefore, confirm that facilitation and suppression processes occur in jackals depending on the large carnivore species and the

**Fig. 3** Average estimated occupancy probability of black-backed jackal (*Canis mesomelas*) across 15 South African protected areas based on the best model. Lines represent the maximum and minimum estimated occupancy per site within PAs (for reserve code, see S1). TSL and TSK are part of the same reserve (TSW), but the former has lions while TSK does not. Codes in parentheses represent the biome of the protected area: nam, Nama Karoo; sav, Savanna; thi, Thicket; suc, Succulent Karoo; fyn, Fynbos



scale. However, we clearly showed that this potential interspecific interaction was not stronger than habitat variables in shaping the geographical variation of jackal's occupancy across South Africa.

### Prediction about effect of anthropogenic features

Jackals may face high levels of persecution and killing in non-protected areas (Blaum et al. 2009; Thorn et al. 2013), and there is evidence that crops could also negatively influence jackals as in the Drakensberg Midlands, South Africa (Ramesh and Downs 2015). Therefore, we expected that anthropogenic factors would impact jackal's occupancy as the surrounding matrix could act as "ecological traps" or population "sinks" (e.g., wild dogs Van Der Meer et al. 2014; black-backed jackals, Minnie et al. 2018), but our investigation did not capture this. Although individual models (i.e., human density, agriculture, and build-up) had a negative effect on jackal's occupancy, these variables were not included in the best models ( $\Delta AIC < 2$ ) suggesting that these factors were not important for this species. Our findings correspond to a study in the Karoo region, where no differences were found between jackals' occupancy rates between a protected area and its surrounding (Drouilly et al. 2018). This could be related to the fact that lethal management (killing) does not affect jackal densities in some areas due to compensatory reproduction and immigration (source-sink dynamics) (Minnie et al. 2018, 2016). Similarly, in some other areas, jackals seem to prefer croplands depending on the season (Humphries et al. 2016). These

different responses show the highly adaptable behavior of jackals which might be one of the reasons the surrounding context around reserves did not influence jackal distribution across the country. We also predicted that jackals may use the reserve as a refuge, periodically moving onto neighboring areas. However, although distance to the fences was included in the best models, this effect was very weak and with high standard errors preventing us from making any inference about potential edge effects.

Kamler et al. (2013) found that the abundance of jackals was related to levels of human persecution with relatively low numbers on private ranches, moderate on a game farm, and relatively high on a nature reserve. Although our approach used agriculture and infrastructure as a proxy for human production, future research should use more specific measures such as density of livestock (Blaum et al. 2009), human activity patterns (Kaunda 2001), and land cover of surrounding, as well as levels of and typologies of persecution (i.e., lethal vs non-lethal predator management strategies), to better evaluate if these factors are related to jackal occupancy within PAs. To our knowledge, this information was not available for all PAs or not up to date to provide meaningful inferences. Our study is likely the first trying to disentangle responses of jackals at large scales targeting several PAs, whereas most research has been conducted at local scales. Complementary research expanding the camera grid outside the PAs might find other camera site level features related to the patterns of jackal occupancy, habitat use, or distributions (e.g., Drouilly et al. 2018).

We selected some landscape factors that could act as surrogates for bottom-up processes based on a specific hypothesis, but other factors not measured in this study could also influence the pattern detected. Hayward et al. (2017), for example, showed that jackal diets are affected by both top-down and bottom-up factors, because apex predators as well as prey size and birthing behavior affected prey preferences of jackals. They found that prey biomass is an important predictor of jackal dietary preferences, but at the same time, jackals showed different diet preferences in the presence/absence of apex predators. Van de Ven et al. (2013) found seasonal variability of jackals' diet, and Brassine and Parker (2012) reported changes in scavenging activities irrespective of apex predator presence. Another potential factor that could affect jackal occupancy is the interspecific competition with other prey species and mesopredators (Bagniewska and Kamler 2013). It is possible, for example, that the importance of open habitats found in this study could be related to the presence of preferable prey species such as Springbok (*Antidorcas marsupialis*) as suggested by Kamler et al. (2019) for a private reserve. All these factors make the study of environment and species interaction among generalist mesocarnivore very complex and context dependant. Our research sheds light on these complex interactions and the potential drivers of jackal distribution at large scales, highlighting the importance of fine-scale habitat structure features irrespective of the surrounding context at the reserve level and top-down control at different scales. Further, the great flexibility of jackals might suggest that management of this species must be addressed at fine scales understanding each local context.

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Park Zoo, and The Living Desert. We are grateful to the anonymous reviewers for their useful feedback.

**Author contribution** All authors contributed to the study conception and design. Data collection followed the standards of Snapshot Safari Project with different volunteers and students participating in these activities, including all co-authors. Data preparation and variable extraction were performed by LEP and GCS, and formal analysis was conducted by LEP with input from GCS and LS. The first draft of the manuscript was written by LEP and all authors provided feedback on previous versions of the manuscript, including the revisions. JAV and HV supported funding acquisition. All authors read, provided feedback, and approved the final manuscript.

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**Data availability** Source data can be accessed from [https://github.com/LainPardo/paper\\_jackal\\_occ\\_SA](https://github.com/LainPardo/paper_jackal_occ_SA) or by direct request to the corresponding author.

**Code availability** [https://github.com/LainPardo/paper\\_jackal\\_occ\\_SA](https://github.com/LainPardo/paper_jackal_occ_SA)

## Declarations

**Ethics approval** This research did not require ethics approval. The methods used do not include manipulation of animal species and no animal ethics approval was needed or permission by an institutional or governmental regulatory body. Our research did not include any invasive technique that required handling or capture of live animals. Our methods were strictly based on camera traps, a non-invasive technique which therefore does not compromise the welfare of our study species. We had all required permissions to access the PAs and private lands during fieldwork.

**Consent to participate** Not applicable, our research does not involve any informed consent from people. However, we did have the permissions from all landowners or managers to conduct the study.

**Consent for publication** We, the authors, have no conflict of interest and we all agree to submit this manuscript to this journal. None of the managers of the PAs imposes any condition regarding publications and we were not tight to any consent or acceptance from them to submit this paper.

**Competing interests** The authors declare no competing interests.

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