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Who's afraid of the big, bad predator? Contrasting effects of apex predator presence on the behaviour of a mesopredator

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ABSTRACT

Context. Mesopredators experience top down pressure from apex predators, which may lead to behavioural changes such as spatial avoidance to reduce both interference and exploitative competition. However, apex predators may also facilitate mesopredators through the provision of carrion, so mesopredators should respond flexibly to the presence of apex predators. **Aims.** We aimed to investigate the drivers of black-backed jackal (*Canis mesomelas*) space use and detection in areas with and without lions (*Panthera leo*). We predicted that jackal detection and space use will be greater if apex predators facilitate rather than suppress them. Additionally, we predicted that in the absence of lions, the relative abundance of small ungulate species may become important drivers of space use and detection, because jackals can switch from scavenging to hunting. Comparatively, in the presence of lions, larger ungulate species will become important drivers of space use and detection as these species become accessible to jackals through scavenging. **Methods.** We used camera-trapping surveys, a single-species, single-season occupancy modelling approach, and the assessment of activity patterns to explore how apex predators influence the presence and probability of use of different sites in the Eastern Cape province of South Africa. **Key results.** Apex predators both positively and negatively affected the detection of jackals, indicating that these mesopredators show behavioural flexibility at the individual site level. There was high overlap between jackal activity patterns in the presence and absence of lions; however, at one site with lions, jackal activity did not peak at night as observed at other sites. **Conclusions.** Our results indicate that jackals demonstrate behavioural flexibility in the presence and absence of apex predators. Importantly, our results show that apex predators can both facilitate and suppress mesopredators, and that their behavioural responses are dependent on site-specific factors. **Implications.** Our findings highlight that sympatric predator behaviours should be based on site-specific behaviours instead of the general patterns observed in more temperate systems.

Keywords: Black-backed jackals, *Canis mesomelas*, detection, mesopredator release, occupancy, space use, top-down effects, trophic cascade.

Introduction

Apex predators may influence ecosystems via top down forcing (Estes *et al.* 2011), regulating lower trophic levels via lethal and non-lethal effects, whereby the presence of predators leads to behavioural changes in lower trophic levels (Lima 1998; Palomares and Caro 1999). Similarly, apex predators impact other predators via exploitative and interference competition, and in extreme cases intraguild predation, which is the killing of potential competitors within the same guild (Prugh and Sivy 2020). Consequently, subordinate guild members can exhibit behavioural changes such as increased vigilance and altered spatiotemporal activity patterns (Brook *et al.* 2012; Clinchy *et al.* 2016) to reduce lethal and non-lethal impacts (Périquet *et al.* 2015; Macdonald 2016). Ultimately, the functional roles of predators can vary considerably, leading to complex trophic interactions (Fleming *et al.* 2017). Understanding the interactions among carnivores (both positive and negative), and the behavioural responses of mesopredators to dominant apex predators, is important for disentangling their respective ecological roles in ecosystems,

which is critical in order to achieve evidence-based conservation strategies (Saggiomo *et al.* 2017). Such evidence is particularly pertinent for smaller canid species because very little is known about their ecological roles (Fleming *et al.* 2017).

According to optimal foraging theory (MacArthur and Pianka 1966) and habitat selection theory (Rosenzweig 1981), mesopredators will select the habitats that provide the highest energetic gain from resources while also minimising the risks of interference and exploitative competition (Lima and Dill 1990). Mesopredators may reduce this risk by responding on a spatial scale, avoiding areas of high risk (Broekhuis *et al.* 2013; Marneweck *et al.* 2021), or temporally, avoiding times when apex predators are most active (Crooks and Van Vuren 1995; Comley *et al.* 2020). Despite the risk of interference competition, mesopredators can also benefit from the presence of apex predators through the provision of carrion and facilitation of scavenging (Moleón *et al.* 2014). Thus, mesopredators are expected to respond flexibly to large carnivore presence, allowing them to balance this trade-off between risk and facilitation. In Alaska, for example, coyotes (*Canis latrans*) spatially avoid areas of high wolf (*Canis lupus*) activity in summer when it is suggested the risk of mortality outweighs the benefits of carrion facilitation, but prefer areas with high wolf activity in winter when metabolic demands are higher and food availability is reduced (Klauder *et al.* 2021). In the absence of apex predators or when carrion is scarce, mesopredators often hunt vulnerable prey (e.g. newborn animals) or small animals (Pereira *et al.* 2013).

The complex balance between mesopredator energetic requirements and risk avoidance can be influenced by the anthropogenic-driven elimination and reintroduction of apex predators into ecosystems (Estes *et al.* 2011). Changes to the predator guild can have dramatic consequences to community structure – changes may cascade throughout food webs (Estes *et al.* 2011). Apex predator reintroductions are ubiquitous throughout South Africa, designed to restore ecosystems to more natural states (Miller *et al.* 1999) and promote ecotourism (Hayward *et al.* 2007). Following these reintroductions, mesopredators are likely to make behavioural adaptions to balance risk avoidance and facilitation of scavenging. Black-backed jackals (*Canis mesomelas*; hereafter, jackals) are a mesopredator species found throughout southern Africa and are commonly found in areas both with and without apex predators (Minnie *et al.* 2016). Jackals facultatively scavenge and thus the presence of apex predators presents both risk and reward. In areas with predators, scavenging from carcasses has been shown to comprise a considerable component of their diet (Fourie *et al.* 2015). In the absence of apex predators, jackals hunt vulnerable prey (Kamler *et al.* 2012*a*; Humphries *et al.* 2015; Drouilly *et al.* 2018), suggesting that jackals may switch foraging strategies in the presence and absence of apex predators.

Although there is some information on the effects of apex predators on jackal behaviour, the information is limited (Minnie *et al.* 2018). Importantly, blanket assumptions on the effects of large carnivores on mesopredators should be avoided (Haswell *et al.* 2017). Studies have investigated the effect of apex predators on the diet of jackal but vary in their findings, with some studies reporting the presence of apex predators has no effect on jackal diet (Brassine and Parker 2012), and others that jackals consume larger prey species (via scavenging) in the presence of apex predators (Fourie *et al.* 2015; Minnie 2016; Drouilly *et al.* 2018). Jackals may adjust their space use to allow for coexistence with apex predators, constantly trading predation risk/competition (Palomares and Caro 1999) for resource acquisition in the process. In the presence of apex predators, jackals avoid certain large carnivore species but are attracted to others (Comley *et al.* 2020), revealing behavioural flexibility in response to species-specific risks and rewards, suggesting that this is a stable evolutionary strategy that allows co-existence. In the Eastern Cape, South Africa, there is limited information about the ecology of jackals and their relationships to lions (*Panthera leo*) and other apex predators. In this area, apex predators such as lions have been reintroduced into small, fenced reserves. Such systems offer a restricted use of space, and apex predators often utilise all areas (Welch *et al.* 2015). Thus, within these fenced areas, spatial avoidance of apex predators may be more challenging for mesopredator species (Meadows *et al.* 2017).

Understanding the drivers of jackal space use is important in the context of species co-existence. Natural experiments provide a means to investigate species space use when experimental manipulation is not possible (Meadows *et al.* 2017). Here, we assess whether or not the drivers of jackal space use and detection vary in the presence and absence of lions. Firstly, in areas with lions, we investigated whether or not these apex predators facilitated or suppressed jackals. We hypothesised that if apex predators facilitate jackal scavenging then they will positively influence the space use and detection of jackals. However, if apex predators suppress jackals, space use and detection will be negatively influenced. Secondly, we aimed to assess the drivers of space use in the absence of lions and hypothesised that in the absence of lions, small ungulate species may become important drivers of space use and detection as jackals may switch from being scavengers to hunters. Lastly, we hypothesised that in the presence of lions, larger ungulate species may become important drivers of space use and detection, as these species become accessible to jackals through scavenging.

Materials and methods

Study sites

We used four sites in the Eastern Cape, South Africa, varying in apex predator presence: (1) Kwandwe Private Game Reserve; (2) Great Fish River Reserve; (3) Kariega Private
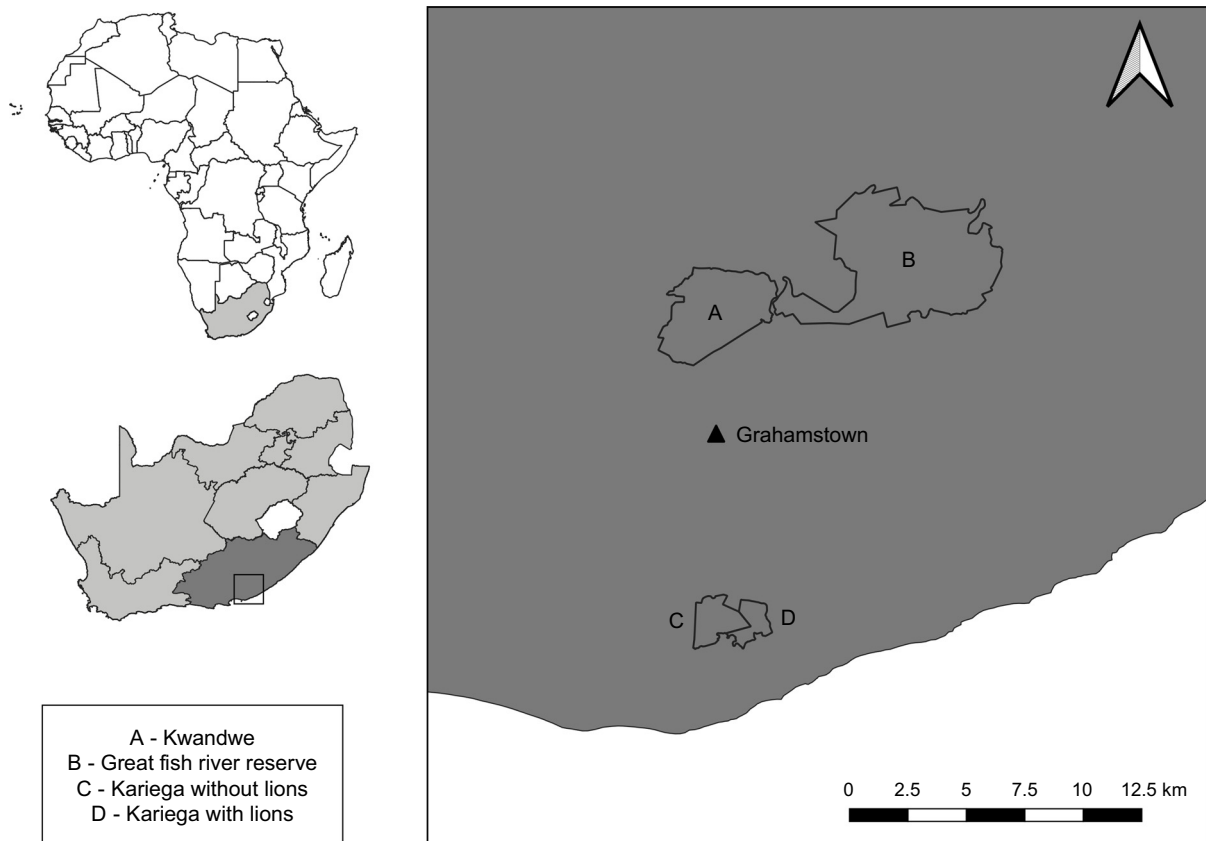
Fig. 1. The locations of the study sites in the Eastern Cape Province, South Africa.

Game Reserve with lions; and (4) Kariega Private Game Reserve without lions. Kwandwe Private Game Reserve (hereafter Kwandwe, between 33°06′S and 26°33′E; Fig. 1) supported reintroduced lions, leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*) and brown hyaenas (*Parahyaena brunnea*). The density of lions was 5/100 km², calculated by dividing the known number of lions by reserve size (Welch and Parker 2016). Great Fish River Reserve (hereafter GFRR, between 33°07′S and 26°39′E; Fig. 1) had not reintroduced any apex predators, but it may have supported low-density, relict, populations of leopards. Kariega Game Reserve (hereafter Kariega, between 35°35′S and 26°37′E; Fig. 1) is divided into four, separate but extensive sections: the eastern section (no lions), the central section (lions), the western section (no lions) and a small section in the south (no lions). The eastern section is separated from the rest of the reserve by a main public road, and the Kariega River separates the central section of the reserve from the western section. For the purpose of this study, only the western (no lions) and central (with lions) sections were considered. The density of lions was 18/100 km². Brown hyaenas are present throughout all sections of Kariega. Leopards have not been reintroduced to the reserve, but a single roaming male leopard has been

infrequently caught on camera traps. All reserves were enclosed in an electric game fence. Although the levels of fence permeability differ for different predators (Williams *et al.* 2021), fences were checked regularly at all four reserves and thus jackals were unlikely to move freely between fenced sections.

Camera trapping

Camera-trapping surveys were conducted at Kwandwe and GFRR between 1 June 2013 and 5 June 2014 (Kok 2016). The total surface area of each camera trapping survey was 36 km², an area large enough to likely contain multiple overlapping resident jackal home ranges based on multiple studies in southern Africa (Rowe-Rowe 1982; Hiscocks and Perrin 1988; Kamler *et al.* 2012*b*, 2019; Humphries *et al.* 2016). At each site, there was a trapping array consisting of nine 4-km² grid cells. Both grids were surveyed for 360 consecutive days. Within each grid cell four random points served as cell replicates. The primary survey lasted 90 days at each random point; thereafter the camera traps were rotated within the cell for another 90 days. This process was repeated until each of the four random points within each grid cell had been sampled. At every camera trap location, a single Cuddeback® Attack

(model 1149) strobe flash camera (Non Typical, De Pere, Wisconsin, USA) was mounted onto trees or iron stakes approximately 50 cm off the ground. Cameras were checked every 30–45 days. Photographs were taken 24 h a day. Photographs at night were taken with a xenon white strobe flash (Meek *et al.* 2014). To increase the likelihood of capturing animal activity, cameras were placed facing gravel paths, waterholes, game paths, vegetation corridors or open areas.

Camera trapping at Kariega took place between 7 October 2019 and 8 January 2020. Two brands of remote sensor cameras (Reconyx Hyperfire HC600 (7), Bushnell Trophy Cam HD Model 11953 (3)) were set up following a systematic grid (3 km^2) system and ran for 94 nights (10 cameras in total). Cameras were programmed to capture photographs 24 h a day, with consecutive photographs being taken in 30-s intervals. Cameras were checked on a monthly basis. Despite the methodologies at each reserve being quite different, they were both suitable for the questions being asked (Shannon *et al.* 2014).

Data analyses

Single-species, single-season occupancy models were used to analyse the probability of jackal occurrence trends (MacKenzie *et al.* 2002). Single-season occupancy models provide estimates of occupancy (Ψ) and detection probability (*p*; probability that a species will be detected given presence). Our study violated the assumption of spatial autocorrelation (i.e. avoid capturing the same individual several times) and independence of camera trap sites, which means that our results will be inferred as area used rather than area occupied (MacKenzie and Nichols 2004).

Biologically relevant covariates were included in our models to avoid biased estimates and to identify factors that most strongly influenced the spatial patterns of jackals (MacKenzie *et al.* 2002). Covariates for each camera site included vegetation cover (normalised difference vegetation index, hereafter NDVI – measured using 8-bit pixel depth aerial images), distance to the nearest road (m) and the relative abundance index (RAI) of lions, leopards, brown hyaenas, small ungulate species – blue duiker (*Philantomba monticola*), bushbuck (*Tragelaphus scriptus*), duiker (*Sylvicapra grimmia*), springbok (*Antidorcas marsupialis*) and impala (*Aepyceros melampus*), and large ungulate species – Cape buffalo *(Syncerus caffer caffer)*, blue wildebeest (*Connochaetes taurinus taurinus*), black wildebeest (*Connochaetes gnou*), eland (*Tragelaphus oryx*), gemsbok (*Oryx gazella*), greater kudu (*Tragelaphus strepsiceros*), mountain reedbuck (*Redunca fulvorufula*), plains zebra (*Equus quagga*), red hartebeest (*Alcelaphus buselaphus caama)* and waterbuck *(Kobus ellipsiprymnus ellipsiprymnus)*. We aim to use large ungulate species in the presence of lions as a surrogate for carrion availability, because in the presence of lion these species become accessible to jackals. Distance to the

nearest road and NDVI values were calculated in ArcMap 10.6. RAIs were calculated as the number of independent events (species camera trap photos separated by at least 30 min) divided by sampling effort and multiplied by 100 (i.e. number of events per 100 days of sampling; Karanth and Nichols 1998). All continuous site covariates were scaled into standardised *z*-scores due to the large range of values present (Bruggeman *et al.* 2015). To avoid multi-collinearity among site covariates, variance inflation factors (VIF; Neter *et al.* 1996) were calculated using the *olsrr* package in R (Fox *et al.* 2020). Covariates with a VIF > 6 were excluded (Micheal and Abiodun 2014).

Jackal detection histories consisting of 1s (detection) and 0s (non-detection) were created for Kwandwe, GFRR, Kariega with lions and Kariega without lions to reflect the presence or absence of jackals at each camera-trap site on each occasion (i.e. maximum value of '1' per 24-h period). The original detection history datasets (Kwandwe and GFRR *n* occasions = 90, Kariega *n* occasions = 94) were collapsed into subsets of data by merging the occasions into intervals of between 2- and 10-day sampling occasions. This was done in accordance with other carnivore occupancy studies (see O'Connell *et al.* 2006; Negrões *et al.* 2010; Erb *et al.* 2012) to ensure model fit without over-compressing the statistical power of the data (Burnham and Anderson 2004; MacKenzie and Bailey 2004). Global occupancy models (i.e. most complex models) that included all contributing covariates were applied to the subsets of data for Kwandwe, GFRR, Kariega with lions and Kariega without lions and tested for goodness-of-fit (MacKenzie and Bailey 2004). Subset data that had the closest overdispersion statistic (*ĉ*) to 1 and an insignificant chi-square probability ($\chi^2 p > 0.05$) indicated maximum model fit and were chosen for further analyses (Mazerolle 2020; Appendix 1). Extreme chi-square values (>4 or ≪1) indicate poor fit of the data (Mazerolle 2020).

A two-step approach was used to examine factors influencing jackal space use. The first step was to model detection probabilities by investigating all possible combinations of site covariates while treating occupancy (Ψ) as constant (i.e. intercept only). To compare the relative fit of models, the overdispersion statistic (*ĉ*) estimated from the global model was used to compute quasi-likelihood information criteria (QAICc: corrected for small sample sizes) by scaling the log-likelihood of each model, for each reserve, by its corresponding *ĉ*-value (Mazerolle 2020). In the case of moderate underdispersion, the value of *ĉ* was set to 1 when calculating QAICc (Mazerolle 2020). The best performing detection probability models were retained and used in subsequent analyses to determine which covariates affected Ψ. Therefore, the second step was to model occupancy probabilities by investigating all possible combinations of site covariates, whereby QAICc was used for model selection. Due to the small sample sizes for Kariega with and without lions, only models containing single site covariates for both detection

and occupancy were tested. The package *unmarked* (Fiske and Chandler 2011) was used to fit models and estimate covariate coefficients for each parameter in R (version 4.0.2, R Development Core Team 2017).

The best approximating models for each reserve were selected using the lowest ΔQAICc scores (<2) and the highest QAICc weights ($w > 0.10$; Burnham and Anderson 2004; Appendix 2). Conclusions about strength of evidence of relationships between covariates and parameters (Ψ and p) were based on 95% confidence interval (CIs) of coefficients and the direction of relationships (Arnold 2010; Appendix 2).

The package *overlap* in R was used to analyse differences in the activity patterns of jackals in Kwandwe compared with GFRR and Kariega with lions compared with Kariega without lions. For each reserve, independent capture events for jackals were allocated to each hour of the day (0000–2300 hours). To quantify activity overlap between Kwandwe and GFRR and Kariega with lions and Kariega without lions, statistical methods developed by Ridout and Linkie (2009) were used. The coefficient of overlap ($\Delta 1$) ranges from 0 (indicates no overlap) to 1 (indicates complete overlap).

Results

In total, 6312 camera trap nights were achieved across the first two sites (3116 at Kwandwe and 3196 at GFRR). No photographic evidence of leopards was captured at GFFR (Table 1). For Kariega, 376 camera trap nights were achieved with lions and 522 camera trap nights were achieved without lions. Two photographs of leopards were captured at one camera trap site in the section without lions (Table 1), but the occupancy analyses could not run with the inclusion of this covariate so it was excluded.

All covariates were retained in the analyses because no covariates exhibited multi-collinearity (VIF < 6). Without collapsing the capture data, 51 unique detections were recorded for jackals at Kwandwe, 489 for GFRR, 39 for Kariega with lions and 27 for Kariega without lions (Table 1). For Kwandwe, the global model fitted the data best when detection histories were collapsed into 2-day intervals

Table 1. Total number of independent events for predator species at Kwandwe, Great Fish River Reserve, Kariega with lions and Kariega without lions (before the collapse of datasets).

Species	Number of events			
	Kwandwe	GFRR	Kariega with lions	Kariega without lions
Lion	4	0	10	0
Leopard	22	0	0	2
Brown hyaena	70	0	5	28
Black-backed jackal	51	489	39	27

(Kwandwe: $n = 40$ detections, $\hat{c} = 1.39$, $\chi^2 p > 0.05$; Appendix 1). For GFRR, the global model fitted the data best when detection histories were collapsed into 10-day intervals (GFRR: $n = 182$ detection, $\hat{c} = 0.97$; $\chi^2 p > 0.05$; Appendix 1). For Kariega with lions, the global model fitted the data best when detection histories were collapsed into 2-day intervals ($n = 26$ detections; $\hat{c} = 1.25$, $\chi^2 p > 0.05$; Appendix 1), and for Kariega without lions, the global model fitted the data best when detection histories were collapsed into 6-day intervals ($n = 18$ detections; $\hat{c} = 1.03$, $\chi^2 p > 0.05$; Appendix 1).

At Kwandwe, there was moderate evidence (Arnold 2010) that the space use of jackals was positively influenced by leopard RAI (Table 2). At GFRR, there was moderate evidence (Arnold 2010) that jackal space use was positively influenced by large ungulate RAI and negatively influenced by small ungulate RAI (Table 2). At both sections of Kariega, the space use of jackals was not influenced by any of the covariates stipulated (Table 2). The expected probability of space use for jackals at each reserve for the top ranking model was 0.37 for Kwandwe, 1.00 for GFRR and 1.00 for both sections of Kariega.

At Kwandwe, jackal detection probabilities were strongly influenced by lions (negatively), brown hyaenas (positively) and large ungulates (negatively) (Table 2). At GFRR, jackal detection probabilities were strongly influenced by large ungulates (positively; Table 2).

In the Kariega section with lions, jackal detection probabilities were strongly influenced by lions (positively), whereas in the section without lions jackal detection probabilities were not influenced by any stipulated covariates (Table 2).

Activity overlap for jackals in Kwandwe and GFRR is considered high (estimated overlap coefficient of 0.80), whereas the activity overlap for jackals in Kariega with lions and Kariega without lions was slightly lower (estimated overlap coefficient of 0.70). The activity peaks for jackals and Kwandwe and GFRR are fairly similar (Fig. 5), whereas at Kariega the activity peaks of jackal with and without lions differed (Fig. 6). In the absence of lions, jackals had an activity peak in the early mornings and evenings, whereas in the presence of lions, jackals only had an activity peak in the early mornings.

Discussion

Our study illustrates the variations in space use shown by jackals in areas with and without lions. Specifically, we found that occupancy models showed moderate evidence that leopard RAI was positively related to jackal space use at Kwandwe, and showed moderate evidence that large ungulate RAI was positively related to jackal space use and small ungulate RAI was negatively related to jackal space

Table 2. QAICc weights (*w*) for covariates from well-supported models (*w* > 0.10 and QAICc < 2) for each dataset.

Parameter	Covariate	Kwandwe	GFRR	Kariega with lions	Kariega without lions
Ψ	Null	0.27		0.99	1.00
	Large ungulate RAI		0.40 (+)[A]		
	Small ungulate RAI		0.39 (−)[A]		
	Leopard RAI	0.11 (+)[A]			
Occu probability		0.37 ± 0.10	See Fig. 3	1.00 ± 0.01	1.00 ± 0.00
P	Null				1.00 (−)[A]
	Lion RAI	0.27 (−)[B]		0.99(+)[B]	
	Large ungulate RAI	0.27 (−)[B]	0.40 (+)[B]		
	Brown hyaena RAI	0.27 (+)[B]			
Detec probability		See Fig. 2	See Fig. 3	See Fig. 4	0.20 ± 0.04

The direction of the relationship for covariates from the best fit models are indicated in parentheses. Occupancy (occu) and detection (detec) probabilities are given for the top performing models for each dataset.
[A]Medium evidence of relationship.
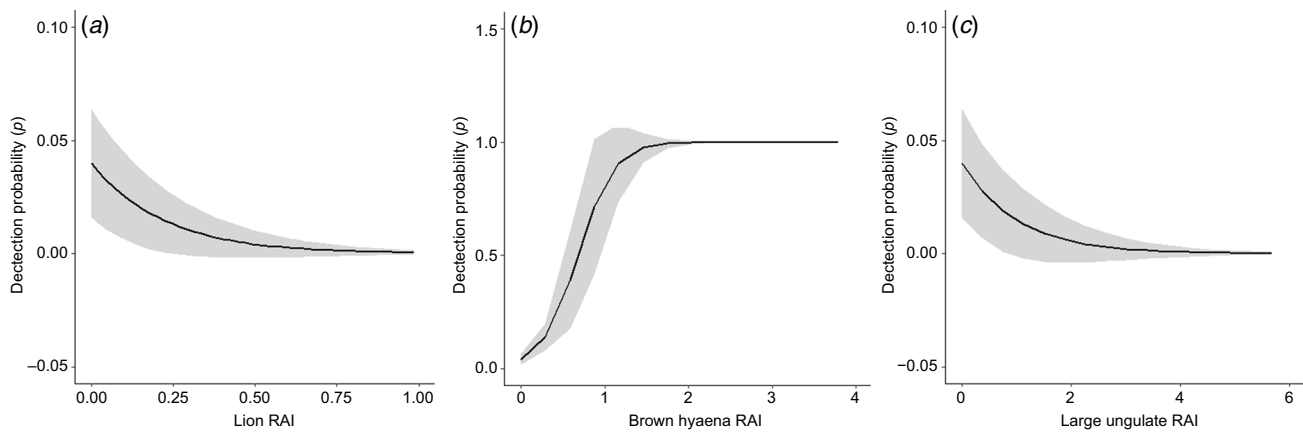[B]Strong evidence of relationship.

Fig. 2. Detection probabilities from the top performing occupancy model for black-backed jackals in Kwandwe Private Game Reserve. The graphs represent strong relationships with the relative abundances (RAI) of (*a*) lions, (*b*) brown hyaenas and (*c*) large ungulates.

use at GFRR. Occupancy models did not suggest any significant factors influencing space use by jackals at Kariega. Different factors affected jackal detectability across our sites, highlighting the importance of site-specific effects. Interestingly, lion RAIs were related to jackal detection at both sites with lions, but with opposing effects.

Camera traps were operational 24 h per day, thus increases in detection could be attributed to increases in local abundance or activity in relation to corresponding covariates (Cove *et al.* 2014). The detection of jackals in the presence of apex predators varied across sites. At sites with lions, lion presence was both positively and negatively related to jackal detection (Table 2). At Kariega, the presence of lions was positively related to jackal detection, but at Kwandwe, lions were negatively related to their detection (Table 2). Lions have been reported to kill jackals (Schaller 1972; Stander 1992), thus the negative effect of lion RAI on jackal detection at Kwandwe is likely attributed to predation risk

effect (see Comley *et al.* 2020) and their avoidance. The density of lions varied considerably across the two sites, with Kariega supporting a much higher density of lions than Kwandwe. Thus, the positive effect of lion RAI on jackal detection at Kariega is intriguing. Other studies have reported that high densities of lions are associated with high densities of jackal species (Durant *et al.* 2011), suggesting a positive effect of this apex predator on this mesopredator species, and that extensive overlap occurs between the two species at the home-range level (Kamler *et al.* 2020). Because the density of lions is much higher at Kariega, jackals may be unable to spatially avoid lion and may use dietary or temporal partitioning instead. Although temporal overlap was high between Kariega sections, in the absence of lions, jackals displayed a peak in activity at night, which was not observed in the presence of lions (Fig. 6). Jackals may avoid high night activity in the presence of lions at Kariega because this is when lions are predominantly active
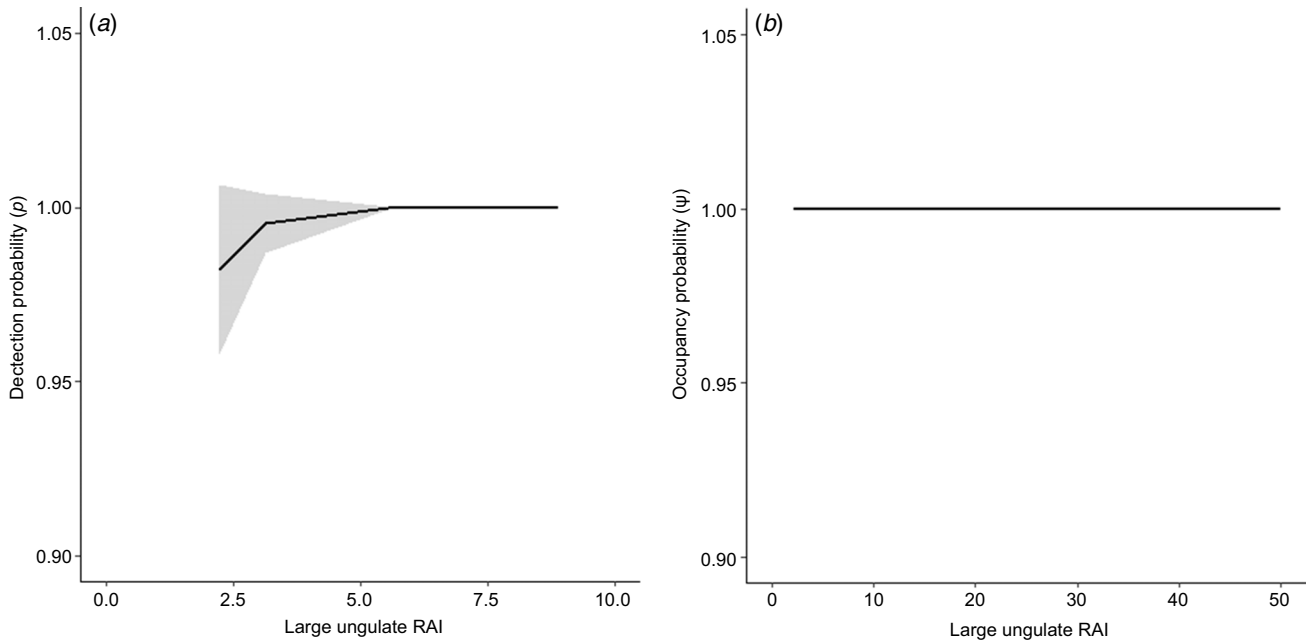
Fig. 3. Detection (*a*) and occupancy/space use (*b*) probabilities from the top performing occupancy model for black-backed jackals in Great Fish River Reserve. The graphs represent strong relationships with the relative abundance (RAI) of large ungulates.
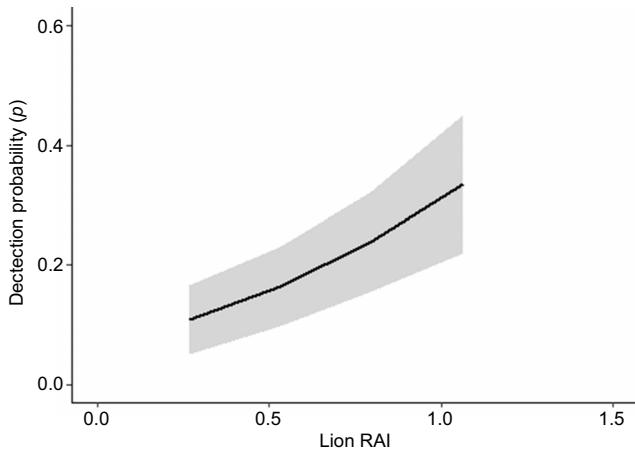

Fig. 4. Detection probability from the top performing occupancy model for black-backed jackals in Kariega Game Reserve with lions. The graph represents a strong relationship with the relative abundance (RAI) of lions.
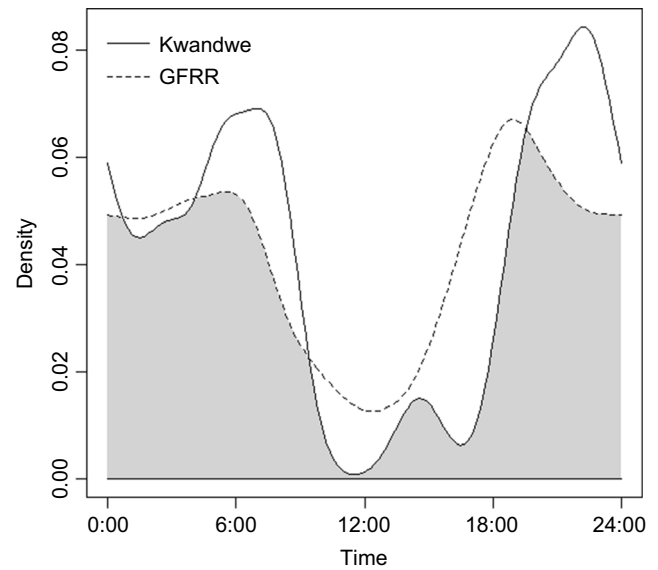

Fig. 5. A comparison of the temporal activity patterns of black-backed jackals at Kwandwe Private Game Reserve (lions present) and Great Fish River Reserve (lions absent) in the Eastern Cape, South Africa.

and hunt (Cozzi *et al.* 2012). Dietary partitioning was beyond the scope of our study.

Leopard RAI and brown hyaena RAI were positively related to jackal space use and detection (respectively) at Kwandwe, whereas these predators had no effect at Kariega (Table 2). The density of brown hyaenas and leopards at Kwandwe are known to be high (Welch and Parker 2016), suggesting that when densities of apex predators are high, facilitation may outweigh suppression. Similar findings were reported by Comley *et al.* (2020), where leopards had a positive

effect on the detection probability of jackals. The density of brown hyaenas and leopards are unknown at Kariega, but the density of leopards is likely to be much lower because unlike Kwandwe, no individuals have been introduced. Although the relative abundance of brown hyaenas was the same at both reserves (0.03), 83% of cameras were placed on roads at Kariega vs none at Kwandwe. Roads have a
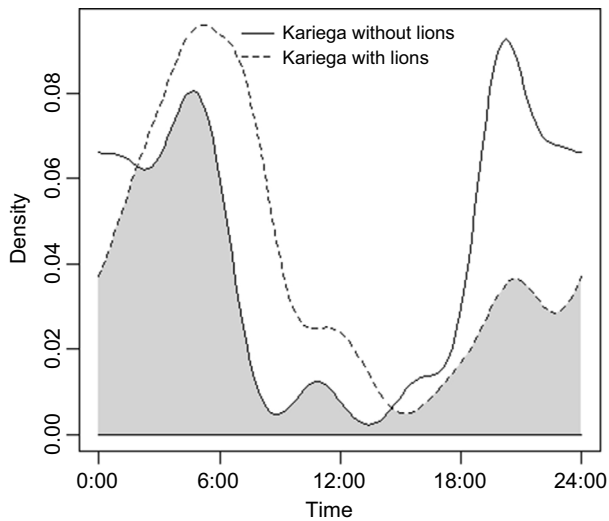
Fig. 6. A comparison of the temporal activity patterns of black-backed jackals at Kariega Game Reserve with and without lions, in the Eastern Cape, South Africa.

positive effect on the detection of brown hyaenas and provide much higher capture rates of brown hyaenas when compared with cameras off roads (Mann *et al.* 2015; Welch and Parker 2016), so the density of brown hyaenas at Kariega is likely to be less than that at Kwandwe.

We expected that large ungulate RAIs may have been positively related to jackal detection in areas with lions, because these species can become an accessible food source via scavenging, but this was not the case. Large ungulates were found to have a negative effect on jackal detection at Kwandwe (lions present) and a positive effect on jackal detection at GFRR (lions absent; Table 2). A possible explanation is that jackals avoid large ungulates or high-density prey areas in the presence of lions to minimise direct competition as seen in other subordinate predators (Durant 1998). Lions have been shown to kill jackals to remove potential competitors (Schaller 1972; Stander 1992) and by avoiding larger ungulates may reduce the risk of intraguild predation. Small ungulates were not an important driver of jackal space use in the absence of large predators. This may be due to minimal hunting of small prey in these areas, because jackals may still rely on carrion from natural mortality. Because jackals are known to scavenge, future studies should aim to quantify carcass presence and availability to assess whether this is an important driver of jackal space use.

The activity patterns of jackals revealed high temporal overlap between sites with and without lions (Figs 5, 6). Patterns were similar between Kwandwe and GFRR where peaks in morning and evening activity were observed (Fig. 5). Differences were observed between Kariega with and without lions in that jackal evening activity peaked in the absence of lions, but was much lower in the presence of

lions (Fig. 6). These results indicate that generalisations about behaviour in the presence and absence of lions should be avoided because periods of activity may differ at the site level.

Our results highlight the importance of site-specific effects, specifically demonstrating that apex predator presence can be both positively and negatively related to the detection of mesopredators and that this can vary at the site level. Lion RAI can be both positively and negatively related to the detection of jackals, and thus facilitation and suppression by this apex predator may be important and may vary at site level, or jackals may avoid apex predators temporally or via dietary separation. Importantly, the data assessed in this study is bycatch data and thus the differences in design between sites and statistics were not optimised to disentangle the effects of lions and jackals. Differences in design and climatic conditions may have influenced results. Lastly, the same camera grid was used to estimate lion and ungulate RAIs. Given the vast differences in ranging patterns, this could have resulted in ungulates being underrepresented in estimates. It is also important to note that differences in historical land use, management practices, neighbouring land size, porosity of the boundary fence and other such factors may have influenced results. Ultimately, future studies should investigate the relationship between lions and jackals in greater detail by assessing jackal behaviour at multiple sites before and after the introduction of lions, and compare this with control sites. Our study shows that apex predators can have contrasting effects on mesopredators and that mesopredators may display behavioural flexibility based on site-level conditions. Importantly, we demonstrate that generalisations about intraguild relations from one site to another should be avoided, and that sympatric predator behaviour should be based on site-specific behaviours instead of general patterns that have been observed in more temperate systems.

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Appendix 1. Goodness-of-fit results from the global occupancy model for each reserve/ section, using different collapsing periods

The chi-square probability ($\chi^2 p$) and overdispersion statistic ($\hat{c}$) were used to choose the best-fit model for each reserve/section and is highlighted in bold. Covariates set for occupancy and detection for each reserve are stipulated in brackets.
Kwandwe (lion relative abundance (RAI), leopard RAI, brown hyaena RAI, small ungulate RAI, large ungulate RAI)

Collapsing period	No. of periods	$\chi^2 p$	$\hat{c}$
Full dataset	90	0.31	0.07
2-day sampling period	**45**	**0.28**	**1.39**
3-day sampling period	30	0.14	1.95
4-day sampling period	22	0.01	4.50

Great Fish River Reserve (distance to road, small ungulate relative abundance (RAI), large ungulate RAI)

Collapsing period	No. of periods	$\chi^2 p$	$\hat{c}$
Full dataset	90	0.00	43.37
9-day sampling period	10	0.98	0.89
10-day sampling period	**9**	**0.30**	**0.97**
11-day sampling period	8	0.70	0.85
12-day sampling period	7	0.88	0.87

Kariega with lions (lion RAI, brown hyaena RAI, small ungulate RAI)

Collapsing period	No. of periods	$\chi^2 p$	$\hat{c}$
Full dataset	94	0.47	0.00
2-day sampling period	**47**	**0.47**	**1.25**
3-day sampling period	31	0.32	1.33
4-day sampling period	23	0.55	0.37

Kariega without lions (brown hyaena RAI, leopard RAI, small ungulate RAI, large ungulate RAI)

Collapsing period	No. of periods	$\chi^2 p$	$\hat{c}$
Full dataset	94	0.44	0
5-day sampling period	18	0.56	0.64
6-day sampling period	**15**	**0.59**	**1.03**
7-day sampling period	13	0.43	1.16

Appendix 2. Top ranked models (*w* > 0.10 and QAICc < 2) for black-backed jackal for each reserve/section, using quasi-likelihood information criterion for small sample size (QAICc), delta QAICc (ΔQAICc), QAICc weight (QAICcwt) and the number of parameters (*K*)

Kwandwe

Model	K	QAICc	ΔQAICc	QAICcwt
Ψ(null)*p*(rai_lg_ungulate + rai_lion + rai_bh)	6	206.82	0.00	0.27
Ψ(rai_leopard)*p*(rai_lg_ungulate + rai_lion + rai_bh)	7	208.57	1.75	0.11
Ψ(rai_lion)*p*(rai_lg_ungulate + rai_lion + rai_bh)	7	208.58	1.76	0.11
Ψ(rai_sm_ungualte)*p*(rai_lg_ungulate + rai_lion + rai_bh)	7	209.54	2.72	0.07

Model-averaged covariate coefficient estimates (and 95% confidence intervals (95% CI)) from the best approximating model from the analyses examining factors related to the space use of black-backed jackals in Kwandwe. Bold estimates indicate that there was a strong association (CIs do not overlap zero) between the covariate and black-backed jackal detection (*p*).

Parameter covariate	Occupancy (Ψ)	Detection (*p*)
null	−0.54(−1.38, 0.30)	
rai_lion		**−4.60 (−6.52, −2.67)**
rai_bh		**4.69 (2.60, 6.77)**
rai_lg_ungulate		**−1.01 (−1.70, −0.31)**

Great Fish River Reserve

Model	K	QAICc	ΔQAICc	QAICcwt
Ψ(rai_lg_ungulate)*p*(rai_lg_ungulate)	5		0.00	0.40
Ψ(rai_sm_ungulate + rai_lg_ungulate)*p*(rai_lg_ungulate)	6		0.08	0.39
Ψ(dist_roadr + rai_lg_ungulate)*p*(rai_lg_ungulate)	6		2.45	0.12

Model-averaged covariate coefficient estimates (and 95% confidence intervals (95% CI)) from the best approximating model from the analyses examining factors related to the space use of black-backed jackals in GFRR. Bold estimates indicate that there was a strong association (CIs do not overlap zero) between the covariate and black-backed jackal detection (*p*).

Parameter covariate	Occupancy (Ψ)	Detection (*p*)
rai_lg_ungulate	49.9 (−48.24, 148.11)	
rai_lg_ungulate		**1.51 (0.95, 2.07)**

Kariega with lions

Model	K	QAICc	ΔQAICc	QAICcwt
Ψ(null)*p*(rai_lion)	4	62.98	0.00	0.99
Ψ(rai_sm_ungulate)*p*(rai_lion)	5	74.97	12.00	0.01

Model-averaged covariate coefficient estimates (and 95% confidence intervals (95% CI)) from the best approximating model from the analyses examining factors related to the space use of black-backed jackals in KGR with lions. Bold estimates indicate that there was a strong association (CIs do not overlap zero) between the covariate and black-backed jackal detection (*p*).

Parameter covariate	Occupancy (Ψ)	Detection (*p*)
Null	7.29 (−30.20, 44.78)	
rai_lion		**1.78 (1.00, 2.55)**

Kariega without lions

Model	K	QAICc	ΔQAICc	QAICcwt
Ψ(null)*p*(null)	3	105.45	0.00	1.00
Ψ(rai_bh)*p*(null)	4	135.45	30.00	0.00

Model-averaged covariate coefficient estimates (and 95% confidence intervals (95% CI)) from the best approximating model from the analyses examining factors related to the space use of black-backed jackals in KGR without lions. Bold estimates indicate that there was a strong association (CIs do not overlap zero) between the covariate and black-backed jackal detection (*p*).

Parameter covariate	Occupancy (Ψ)	Detection (*p*)
Null	8.97 (−62.07, 80.01)	
Null		*−1.39 (−1.90, −0.87)*