# Facilitation of a free-roaming apex predator in working lands: Evaluating factors that influence leopard spatial dynamics and prey availability in a South African biodiversity hotspot

**Eugene Greyling** [Corresp., Equal first author, 1, 2], **Jessica Comley** [Equal first author, 3], **Michael Cherry** [1], **Alison Leslie** [4], **Lana Müller** [2]

[1] Department of Botany & Zoology, Stellenbosch University, Stellenbosch, Western Cape, South Africa

[2] The Cape Leopard Trust, Cape Town, Western Cape, South Africa

[3] Wildlife and Reserve Management Research Group, University of Mpumalanga, Mbombela, Mpumalanga, South Africa

[4] Department of Conservation Ecology & Entomology, Stellenbosch University, Stellenbosch, Western Cape, South Africa

Corresponding Author: Eugene Greyling
Email address: eugene@capeleopard.org.za

Apex predators ideally require vast intact spaces that support sufficient prey abundances to sustain them. In a developing world, however, it is becoming extremely difficult to sustain large enough areas to facilitate apex predators outside of protected regions. Free-roaming leopards (*Panthera pardus*) are the last remaining apex predator in the Greater Cape Floristic Region, South Africa, and face a variety of threats, including competition for space and resources with humans. Land modification affects species diversity, but little is known about how this impacts African leopards in agricultural landscapes. Using camera-trap data, our study investigated the influence of anthropogenic land modification on leopards and the availability of their natural prey species in two contrasting communities - primarily protected (Cederberg) and agriculturally transformed (Piketberg). Potential prey species composition and diversity were determined, to provide a baseline understanding of prey availability for each region. Factors influencing space-use and detection behaviour of leopards and their main prey species were also assessed. Estimated potential prey species richness (Cederberg = 27, Piketberg = 26) and diversity indices (Cederberg - H’ = 2.64, Ds = 0.90; Piketberg - H’ = 2.46, Ds = 0.89) were found to be fairly similar across the two regions. Furthermore, both the Jaccard’s Index (J = 0.73) and Sørensen’s Coefficient (CC = 0.85) suggested high levels of similarity. Both regions accounted for all main leopard prey species, but their relative abundances (i.e. evenness) in each community differed. Leopards were found to persist across the agriculturally transformed landscape despite these perceived differences. Occupancy modelling revealed that the spatial dynamics of leopards differed between the two regions, except for both populations preferring areas further away from human habitation. Overall, anthropogenic factors played a larger role in affecting spatial utilisation by leopards and their main prey species in the transformed

region, whereas environmental factors had a stronger influence in the protected region. We argue that greater utilisation of alternative main prey species to those preferred in the protected region, including livestock, likely facilitates the persistence of leopards in the transformed region, and believe that this has further implications for human-wildlife conflict. Our study provides a baseline understanding of the potential direct and indirect impacts of agricultural landscape transformation on the behaviour of leopards and shows that heavily modified lands have the potential to facilitate biological diversity, including apex predators. We iterate that conservation measures for the persistence of apex predators should be prioritised where they are present on working lands, and encourage the collaborative development of customised, cost-effective, multi-species conflict management approaches that facilitate coexistence.

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Eugene Greyling*[1,2,a] | Jessica Comley*[3,b] | Michael Cherry[1] | Alison Leslie[4] | Lana Müller[2,c]

Corresponding Author: E. Greyling
Email: eugene@capeleopard.org.za / egreyl98@gmail.com

ORCID ID's:
E. Greyling - 0000-0003-1471-9545
J. Comley - 0000-0002-3043-7022
M.I. Cherry - 0000-0002-5161-7735
A.J. Leslie - 0000-0003-1683-0474
L. Müller - 0000-0001-7842-2041

**Affiliations**
* Shared first authorship
[1] Department of Botany & Zoology, Stellenbosch University, Matieland, Western Cape, 7602, South Africa
[2] The Cape Leopard Trust, P.O. Box 31139, Tokai, Cape Town, 7966, South Africa
[3] Wildlife and Reserve Management Research Group, University of Mpumalanga, Mbombela, 1200, South Africa
[4] Department of Conservation Ecology & Entomology, Stellenbosch University, Matieland, Western Cape, 7602, South Africa

*Current:*
[a] Department of Conservation Ecology & Entomology, Stellenbosch University, Matieland, Western Cape, 7602, South Africa; The Cape Leopard Trust, P.O. Box 31139, Tokai, Cape Town, 7966, South Africa
[b] Department of Environmental and Life Sciences, Universiti Brunei Darussalam, Brunei Darussalam, BE 1410
[c] Justdiggit Foundation, P.O. Box 224-00502, Karen, Nairobi, Kenya

## Abstract

Apex predators ideally require vast intact spaces that support sufficient prey abundances to sustain them. In a developing world, however, it is becoming extremely difficult to sustain large enough areas to facilitate apex predators outside of protected regions. Free-roaming leopards (*Panthera pardus*) are the last remaining apex predator in the Greater Cape Floristic Region, South Africa, and face a variety of threats, including competition for space and resources with humans. Land modification affects species diversity, but little is known about how this impacts African leopards in agricultural landscapes. Using camera-trap data, our study investigated the influence of anthropogenic land modification on leopards and the availability of their natural prey species in two contrasting communities - primarily protected (Cederberg) and agriculturally transformed (Piketberg). Potential prey species composition and diversity were determined, to provide a baseline understanding of prey availability for each region. Factors influencing space-use and detection behaviour of leopards and their main prey species were also assessed. Estimated potential prey species richness (Cederberg = 27, Piketberg = 26) and diversity indices (Cederberg - H' = 2.64, Ds = 0.90; Piketberg - H' = 2.46, Ds = 0.89) were found to be fairly similar across the two regions. Furthermore, both the Jaccard's Index (J = 0.73) and Sørensen's Coefficient (CC = 0.85) suggested high levels of similarity. Both regions accounted for all main leopard prey species, but their relative abundances (i.e. evenness) in each community differed. Leopards were found to persist across the agriculturally transformed landscape despite these perceived differences. Occupancy modelling revealed that the spatial dynamics of leopards differed between the two regions, except for both populations preferring areas further away from human habitation. Overall, anthropogenic factors played a larger role in affecting spatial utilisation by leopards and their main prey species in the transformed region, whereas environmental factors had a stronger influence in the protected region. We argue that greater utilisation of alternative main prey species to those preferred in the protected region, including livestock, likely facilitates the persistence of leopards in the transformed region, and believe that this has further implications for human-wildlife conflict. Our study provides a baseline understanding of the potential direct and indirect impacts of agricultural landscape transformation on the behaviour of leopards and shows that heavily modified lands have the potential to facilitate biological diversity, including apex predators. We iterate that conservation measures for the persistence of apex predators should be prioritised where they are present on working lands, and encourage the collaborative development of customised, cost-effective, multi-species conflict management approaches that facilitate coexistence.

## Introduction

Apex predators are generally large carnivores that can act as keystone species and as such, they have been labelled as ecosystem engineers (Palazón, 2017). One way in which apex predators primarily influence ecosystems is by exhibiting prey species control (Terborgh, 1988; Miller et al., 2001): they can directly reduce prey species numbers by predating on them (reducing competitive exclusion among herbivores, thus inducing greater diversity), but also by influencing them indirectly through behavioural changes, which affect ecosystem resources (Miller et al., 2001; Frank, 2008; Estes et al., 2011; Rosenblatt et al., 2013). Therefore, the local extinction of apex predators within ecosystems can often bear drastic trophic cascade consequences (Terborgh et al., 2001; Hebblewhite et al., 2005; Ripple et al., 2014; 2016; Suraci et al., 2016). For example, biodiversity can be reduced (Estes et al., 2011); the transmission of infectious diseases to humans can increase (Keesing et al., 2010); and damages to crops can increase (Brashares et al., 2013). Apex predators also tend to be seen as charismatic species sought after by tourists and hunters (Lindsey et al., 2007; van der Meer, Badza & Ndhlovu, 2016) and therefore hold an important economic value to society. Thus, the disappearance of apex predators from ecosystems is likely to stimulate knock on effects which may adversely impact human wellbeing (Díaz et al., 2006; Estes et al., 2011).

Traditionally, it was believed that vast, relatively intact ecosystems were required to effectively support viable apex predator populations (Sillero-Zubiri & Laurenson, 2001; Morrison et al., 2007). Their high trophic position and large body size suggests that they require extensive home ranges which sustain sufficient prey abundance (Morrison et al., 2007; Ripple et al., 2014). These spatial requirements often bring apex predators into conflict with humans (Inskip & Zimmerman, 2009; Nyhus, 2016) as they are amongst the first species to be affected by the expansion of human populations and associated cultivation of previously untouched habitats (Morrison et al., 2007; Ripple et al., 2014; Aebischer et al., 2020). A species that is influenced by such anthropogenic activities across the globe is the leopard (*Panthera pardus*; Linnaeus, 1758). Leopards are the most widespread large felid and occur through much of Africa and tropical Asia (Nowell & Jackson, 1996; Stein et al., 2020). They are highly adaptable and successfully occupy a large variety of habitats across their range (Jacobson et al., 2016; Stein et al., 2020), including areas alongside large urban spaces (Kuhn, 2014). However, their ability to occupy areas in such close proximity to humans makes them particularly susceptible to competition with humans for space and resources, inevitably placing leopards at great risk.

Globally, leopards are considered as Vulnerable as their populations are declining and they face multiple threats to their survival (IUCN Red List of Threatened Species; Stein et al., 2020). An estimated 75% of their historic range has been lost (Jacobson et al., 2016), where the average loss for large carnivore species is only around 53% (Ripple et al., 2014). Although suitable habitat in southern Africa, which arguably hosts the healthiest leopard population across its range (Stein et al., 2020), remains widely distributed, it is highly fragmented, having experienced

~51% decline since 1750 (Jacobson et al., 2016). Anthropogenic activities, in particular agricultural practices, are primarily responsible for this fragmentation (Swanepoel et al., 2013). Brink & Eva (2009) have shown that agricultural land increased by 57% at the expense of natural vegetation in sub-Saharan Africa in only 25 years (1975-2000). In South Africa, ~68% of remaining habitat suitable for leopards occurs in non-protected areas that are naturally susceptible to land-use transformation (Swanepoel et al., 2013). Leopards in non-protected areas are most at risk of being killed by human-induced causes such as snares, hunts, poison, or motor vehicle collisions (Balme, Slotow & Hunter, 2010; Swanepoel et al., 2013; 2015). Unfortunately, most published research on leopards in South Africa has taken place inside protected areas (Balme et al., 2014), and inadequate data jeopardizes the conservation of the species on working lands. Thus, it is vitally important that conservation measures be established to accommodate and preserve free-roaming leopards in non-protected transformed regions (Balme, Slotow & Hunter, 2010; Swanepoel et al., 2013; Swanepoel, Somers & Dalerum, 2015).

Free-roaming leopards are the last remaining apex predator found in the Cape Floristic Region (including Fynbos and Renosterveld) and Succulent Karoo Region, which are both biodiversity hotspots and together form the Greater Cape Floristic Region (Born, Linder & Desmet, 2007), in the Western Cape province of South Africa (Martins & Martins, 2006). The human population of the Western Cape (±55 people per $km^2$; Statistics South Africa, 2021) has consistently grown at a faster rate than the national population (Partridge, Morokong & Sibulali, 2021), and almost 90% of the total area of the province is regarded as potential agricultural land. Leopards within this region generally occupy significantly larger home ranges (Patterson, 2008) and occur at much lower densities (Martins & Martins, 2006) than leopards found elsewhere in Africa (excluding the Kgalagadi; Mizutani & Jewell, 1998; Bothma & Bothma, 2012). These leopards are also generally considered smaller than most leopards found elsewhere in Africa (Stuart, 1981; Martins & Martins, 2006) and across the species range (excluding Arabian leopard; Spalton & Al Hikmani, 2006). The Western Cape is therefore an ideal study location to investigate the influence of humans, both directly and indirectly, on this apex predator.

The aforementioned characteristics of leopards in the Western Cape all presumably reflect adaptation to a different diet (Martins et al., 2010). With a great diversity in habitat usage, leopards opportunistically hunt a wide range of prey, depending on local and temporal availability (Hayward et al., 2006). A decline in their primary prey base can, however, impact leopard population structure (Marker & Dickman, 2005; Ray, Hunter & Zigouris 2005; Wolf & Ripple, 2016), and may also affect human-wildlife conflict levels (Khorozyan et al., 2015). Human-wildlife conflict between farmers and leopards in the Western Cape has long been prevalent (Martins & Martins, 2006; Nieman, Wilkinson & Leslie, 2020). Leopards in this region are not only deemed responsible for livestock losses (C. Luyt, 2020, Community Outreach Officer - Cape Leopard Trust), but direct conflict also exists between crop farmers and leopard prey species, often regarded as crop raiders (Norton, 1980; Kingdon, 1982; Estes, 1991; Skinner & Chimimba, 2005). The primary (main) natural prey base for leopards across the Western Cape

include common duiker (duiker; *Sylvicapra grimmia*, Linnaeus, 1758), Cape grysbok (grysbok; *Raphicerus melanotis*, Thunberg, 1811), klipspringer (*Oreotragus oreotragus*, Zimmermann, 1783), and grey rhebok (rhebok; *Pelea capreolus*, Forster, 1790), as well as rock hyrax (hyrax; *Procavia capensis*, Pallas, 1766), Cape porcupine (porcupine; *Hystrix africaeaustralis*, Peters, 1852), and chacma baboons (baboon; *Papio ursinus*, Kerr, 1792) (Martins et al., 2010; Drouilly, Nattrass & O'Riain, 2018; Mann et al., 2019; Müller et al., 2022a). In addition, most of these species are targeted by humans for the illegal harvesting of bushmeat through snare captures in the province (Nieman et al., 2019). A similar competitive relationship between humans and leopards has been documented in the Congo Basin (Henschel et al., 2011), with seemingly negative consequences for leopards. Illegal hunting, which impacts prey species availability, is a continuous concern for wildlife worldwide (Lindsey et al., 2013; Heurich et al., 2018). Besides, snares can also be responsible for the direct capture of leopards resulting in injury or death (Swanepoel et al., 2015; Williams et al., 2017; Nieman, Leslie & Wilkinson, 2019; Gubbi, Kolekar & Kumara, 2021).

As the last remaining apex predator of the Western Cape, free-roaming leopards are expected to be sensitive to changes in prey species populations. But little is known about the extent to which this relationship is influenced by humans. Several studies investigating the drivers of leopard occurrence, density, or ranging behaviour (e.g. Jiang et al., 2015; Allen et al., 2020; Searle et al., 2020; Snider et al., 2021; Loveridge et al., 2022), and predator-prey overlap (e.g. Dias, de Campos & Rodrigues, 2018; Havmøller et al., 2020; Palei et al., 2021; Sehgal et al., 2022; Zaman et al., 2022), have been performed worldwide. However, until relatively recently, few studies have investigated African leopard ecology in human-disturbed landscapes (e.g. Marker & Dickman, 2005; Williams et al., 2017; Strampelli et al., 2018), particularly in commercial agricultural regions. Furthermore, limited direct comparisons of predator populations between protected and non-protected regions have been made (e.g. Swanepoel, Somers & Dalerum, 2015; Drouilly, Nattress & O'Riain, 2018; Curveira-Santos et al., 2020; Faure et al., 2021). Understanding the factors which could best enable the persistence of an apex predator in agriculturally transformed environments, including variables affecting the availability of their natural prey species, are vital to aid management decision making and account for in cost-benefit models that aim to minimise conflict. Inferences about spatial variation in species composition and diversity are also important, both to ecological hypotheses about structure and function of communities and to community-level conservation management (Nichols et al., 1998).

Our study investigated potential prey species diversity, community structure, and factors affecting the behaviour of leopards of the Western Cape and their main prey species, in both an agriculturally transformed and a largely protected landscape, using camera-trap data. First, we aimed to determine whether any real differences exist with reference to potential prey species found in each community and whether any such difference is reflected in the respective leopard subpopulations. Second, we aimed to evaluate and compare factors affecting space-use and detection behaviour of leopards and their main prey in each region. We predicted a greater

diversity of potential leopard prey species to exist in the protected community, as well as differences in community structure. Relative leopard and prey abundances in the protected wilderness region were predicted to be higher than in the transformed agricultural region. And anthropogenic factors were expected to negatively influence habitat utilisation of leopards, as well as their main prey species, across the greater landscape.

## Materials & Methods

### Ethical statement

Relevant permissions to conduct our research were granted by the Social, Behavioural and Education Research Ethics Committee at Stellenbosch University (Project ID #15315), CapeNature (Permit #CN44-59-12321), and in writing by all landowners involved.

### Study area

The Piketberg region (hereafter Piketberg) encompasses a transformed landscape that is primarily characterised by mixed agricultural practices. Our study area is located approximately 130 to 160 km north of Cape Town, South Africa, and situated southwest of the Cederberg region (Figure 1). The survey area was approximately 1500 $km^2$ in size (53 - 864 metres above sea level), covering 55 privately owned mixed agricultural farms extending north from the town of Piketberg to Paleisheuwel, with Citrusdal in the east and Aurora on the western boundary (Figure 1). The area consists of natural vegetation forming a mosaic, highly fragmented by livestock (e.g. cattle (*Bos taurus,* Linnaeus, 1758), horses (*Equus ferus caballus,* Linnaeus, 1758), sheep (*Ovis aries,* Linnaeus, 1758), goats (*Capra hircus,* Linnaeus, 1758), pigs (*Sus domesticus,* Erxleben, 1777)), fruit, and other crop farmlands in and around mountainous terrain (Linder, 1976; Mucina & Rutherford, 2006).

The Cederberg region (hereafter Cederberg), known for its rugged remoteness, is a largely protected area first proclaimed in 1973 and located 200 to 250 km northeast of Cape Town (Figure 1). The survey area was approximately 1700 $km^2$ in size (254 - 1455 metres above sea level) and included the Matjiesrivier Nature Reserve and the Cederberg Wilderness Area. Both areas are formally protected and managed by the provincial conservation regulation body and authority in the Western Cape, known as CapeNature (Figure 1). Privately owned areas included were Bushmans Kloof Wilderness Reserve, community owned land used for the harvesting of rooibos and limited pastoralism by subsistence farmers, and the Cederberg Conservancy, consisting of pro-conservation farms that are used for ecotourism and largely kept in a natural ecological state. The two main biomes present are Fynbos and Succulent Karoo in mountainous terrain (Mucina & Rutherford, 2006).

[Insert Figure 1 here]

The Western Cape has a Mediterranean type climate characterised by hot, dry summers and cold, wet winters (Cowling & Holmes, 1992). Localised climatic conditions vary across the greater study area because of its mountainous nature, and the vastness of the landscape makes it extremely difficult to describe the climate of the study area in general terms. In essence, average annual rainfall appears slightly higher, and average summer air temperatures somewhat lower in Piketberg compared to the Cederberg (Climate-Data.org, 2020). Average winter air temperatures are more uniform across both regions, but snowfall is more abundant in the Cederberg which is generally at a higher altitude (Climate-Data.org, 2020).

## Field sampling methods

### *Camera-trap surveys*

Single season (dry summer – November to March) subsets of detection and non-detection data that were collected in the Cederberg (2017-2018) and Piketberg (2019-2020) were used for our study. The 73 camera-trap stations (n = 146 cameras) in the Cederberg were all located within areas with protected status, whereas the 64 camera-trap stations (n = 128 cameras) in Piketberg were situated in non-protected areas nestled between and on farmlands (Figure 1). Paired motion and heat detecting Cuddeback X-Change series camera-traps were used at each camera station during both surveys. Our setup procedures followed standard protocols optimised for the detection of leopards, whereby the landscape across both study regions was divided into 50 $km^2$ blocks (Figure 1), based on the minimum estimated home range size recorded for a female leopard with cubs in the Western Cape (37 $km^2$; Martins, 2010; also see Müller et al., 2022a; 2022b). Camera-trap stations were dispersed across mountainous habitat with mean distances of 2.78 km (Cederberg) and 3.09 km (Piketberg) between individual stations and two to three stations per block (Figure 1). Camera-trap locations were selected based on the presence of tracks and signs of leopards and their main natural prey species found in the nearby vicinity on initial site investigation. Cameras were mounted ~40 cm above the ground and perpendicular to a game trail, road, or drainage line. Camera-traps were serviced at an interval of about eight weeks to download images, change batteries, perform site data collection (i.e. recording covariates around each site), and for general maintenance.

### *Covariate data*

Environmental (i.e. altitude, vegetation type, vegetation age, nearest water source type and its distance) and anthropogenic (i.e. distances to the nearest road and human habitation, evidence of disturbance, livestock and hunting) covariates surrounding each camera-trap station were recorded during each servicing period (see Supplementary Material, Table S1). Some categorical and binomial covariates were determined with a repeated physical site inspection of the surroundings performed by a trained and experienced individual covering a 100 m radius around each station (Table S1). Other variables were determined by a combination of physical investigation, with recordings made using a GPS unit (Garmin ETrex 10), and local knowledge

(Table S1). Any further verification was performed using Google Earth (Google, n.d.) and historical fire records (Table S1). The chosen covariates reflect natural and human-induced factors that could influence predator and prey space-use or detection at each site. Tracks and signs of all mammalian wildlife species found and positively identified during the site inspections were also recorded.

## Data analyses

### *Camera-trap data*

Camera Base software (Tobler, 2010) was used to process images and extract meta-image information from each photograph (image name, date, and time) while correcting for any time stamp errors. Faunal species and number of individuals in each photograph was identified where possible. Primary analyses were performed using the Camera Trap Analysis Package (CTAP) software developed by the Zoological Society of London (Amin & Wacher, 2017). Only terrestrial mammals > 0.5 kg, including leopard (see Charsley (1977), Steyn & Funston (2006), and Balme & Hunter (2013) for examples of reported cannibalism), were considered as potential leopard prey species for analyses as they are the main target group for camera-traps set up in this manner, and are also generally regarded as the main dietary component of leopards (Hayward et al., 2006; Tobler et al., 2008; Martins et al., 2010; Drouilly, Nattrass & O'Riain, 2018; Mann et al., 2019; Müller et al., 2022a). Relative abundance indices (RAI; i.e. number of events, where an "event" is defined as any image sequence for a given species occurring after an interval of ≥ 60 minutes from a previous sequence of that species, per 100 days of camera trapping; Karanth & Nichols, 1998; Amin et al., 2018) per camera-trap station were calculated for known main prey species of leopards in the study area, sympatric meso-carnivores - caracal (*Caracal caracal*, Schreber, 1776) and black-backed jackal (*Canis mesomelas*, Schreber, 1775) - and leopards, and used as biotic covariates for the occupancy models (Table S1). Despite being influenced by sampling design or species' behaviour (Sollmann et al., 2013), RAI is still considered a suitable tool for assessing species occurrence (Hedwig et al., 2018; Palmer et al., 2018).

### *Community structure*

Biological communities can differ in species composition, total number of species (richness), and the relative abundance of species (evenness) (Colwell, 2009). Species diversity refers to a community level concept that integrates both richness and evenness (Colwell, 2009). Species sample-based rarefaction curves were constructed and the terrestrial medium-to-large (> 0.5 kg) mammal species richness (*S*) - representing potential leopard prey species - was estimated for each surveyed community using a non-parametric incidence-based estimator Jackknife with order one (Bunge & Fitzpatrick, 1993). Livestock and other domestic species were excluded from analyses. Simpson's (*Ds*) and Shannon-Wiener (*H'*) diversity indices were calculated for each community using RAI values in the package 'vegan' in R statistical software (see Table S2; Oksanen et al., 2019). Simpson's diversity index is most sensitive to changes in more common

highly abundant species, while the Shannon-Wiener diversity index is most sensitive to changes in rare less abundant species (Magurran, 2004). Community structure plots representing the RAI as a factor of trophic level and mean adult body weight of potential prey species were also constructed. Jaccard's Index ($J$) and the Sørensen's Coefficient ($CC$) were calculated as measures of similarity, directly comparing Piketberg and the Cederberg, using the following formulae:

$$J = \frac{A}{[A + B + C]} \qquad CC = \frac{2A}{[2A + B + C]}$$

$A$ = Number of species shared by two communities,
$B$ and $C$ = Number of species unique to each of the two communities, respectively.

The latter places more emphasis on the shared species present rather than the unshared and retains sensitivity in more heterogeneous data sets. Sørensen's ecological distance ($D_{CC}$ = 1-$CC$) is therefore useful as many species may potentially be present in a community, but not present in a sample from that community (Magurran, 2004).

*Occupancy modelling*

Naïve occupancy, defined as the proportion of sites that recorded at least one photograph of the target species, was calculated for leopards of each community:

$$\psi_{naïve} = \frac{\#\ of\ sites\ detected}{\#\ of\ sites\ sampled}$$

To accurately model occupancy, unique detection histories consisting of 1s (detection) and 0s (non-detection) were created for leopards and their main prey species (i.e. baboon, duiker, grysbok, hyrax, klipspringer, porcupine, and rhebok) in the Cederberg and Piketberg. The unique detection histories reflected the presence or absence of each species at each camera-trap site on each occasion (maximum value '1' per 24 hr period) for each region. Original unique detection history datasets (Cederberg N occasions = 151; Piketberg N occasions = 132) for each species were collapsed into data subsets by merging the occasions into intervals of between five to 11-day sampling occasions. This was deemed appropriate as it reduced each species dataset into manageable sizes for computational purposes and accurately represented the rarity of the study species (Sollmann, 2018).

All continuous covariate values were scaled into standardized z-scores (Bruggeman et al., 2016). Multi-collinearity was tested for by calculating variance inflation factors (VIF), whereby covariates with VIF scores greater than three were removed (Wang et al., 2018). A global occupancy model that included all ecologically relevant covariates (see Table S1) was applied to the subsets of data for each species and tested for goodness-of-fit (MacKenzie & Bailey, 2004).

Subset data for each species that had the closest over dispersion statistic (ĉ) to 1 (extreme values over (> 3) or under 1 (< 0.90) indicate poor fit of the data) and an insignificant chi-square probability ($\chi^2 p > 0.05$), was chosen for further occupancy analyses (see Table S3; Mazerolle, 2017). This showed maximum model fit without over compressing statistical power of the data (Burnham & Anderson, 2004; MacKenzie & Bailey, 2004). Our study violates the assumption of spatial autocorrelation and independence of camera-trap sites, which means that our results will be interpreted as area (i.e. space) used rather than area occupied (MacKenzie & Nichols, 2004).

For each species, only combinations of covariates that could affect the two parameters (space-use probability, ψ, and detection probability, *p*) and that presented ecologically reasonable hypotheses were included (McDonald et al., 2016). With such a large number of covariates, the set of candidate models that we might have examined was extremely vast (Schuette et al., 2013). Therefore, we used a stepwise procedure following Dugger, Anthony & Andrews (2011), whereby the first step was to model *p* by investigating additive combinations of covariates while treating ψ as constant (i.e. intercept only). For model selection, the over dispersion statistic (ĉ) estimated from the global model for each species was used to compute quasi-likelihood information criteria (QAICc: for small sample sizes) by scaling the log-likelihood of each model, for each species, by its corresponding ĉ value (Mazerolle, 2017). Therefore, QAICc model-selections were used to retain the best *p* model for each species to use in subsequent analyses of factors affecting ψ. The second step was to model ψ by investigating additive combinations of covariates. The package 'unmarked' (Fiske & Chandler, 2011) was used to fit models and to estimate covariate coefficients for each parameter in R (version 4.1.2, R Development Core Team, 2017). The R package 'AICcmodavg' was used for all model selection computations (Mazerolle, 2017).

The lowest △QAICc scores (< 2) and highest QAICc weights ($w > 0.10$) were used to select the best-approximating models for each species in each community (see Table S4 & S6; Burnham & Anderson, 2004). We drew conclusions about strength of evidence of relationships between covariates and parameters based on 95% confidence intervals (CIs) of coefficients and the direction of relationships (see Table S5 & S7; Arnold, 2010).

## Results

A total of 10114 operational camera-trap days (mean 140 days/station) were accumulated in the Cederberg, with only one station failure (refer to Figure 1). In Piketberg, 6258 operational camera-trap days (mean 103 days/station) were accumulated, and three camera-trap stations failed (Figure 1). The outcomes of our study are unlikely to be affected by this difference as sampling effort across both regions was sufficient (see Figure 2) and indices based on relative abundance values were employed, providing equal weight to both communities, therefore allowing comparison.

*Species richness*

Cederberg had an estimated potential prey species richness ($S$ = 27) similar to that of Piketberg ($S$ = 26). The rarefied species accumulation curves do however show more species detected per unit effort in the Cederberg compared to Piketberg (Figure 2). Both the Shannon-Wiener ($H'$) and Simpson diversity ($Ds$) indices were only marginally higher in the Cederberg ($H'$ = 2.64, $Ds$ = 0.90) compared to Piketberg ($H'$ = 2.46, $Ds$ = 0.89). Thirty potential natural prey species were photographed across the two regions (Cederberg: 27; Piketberg: 25), with Cederberg having five unique species and Piketberg three (Table S2).

[Insert Figure 2 here]

*Community structure*

Differences in community structure were largely complementary, providing a similar pattern across trophic guilds for both the Cederberg and Piketberg (Figure 3). The same number of carnivore species were detected in both areas (n = 10), but no Cape fox (*Vulpes chama*, Smith, 1833) or large grey mongoose (*Herpestes ichneumon*, Linnaeus, 1758) were recorded in the Cederberg, whereas black-backed jackal and water mongoose (*Atilax paludinosus*, Cuvier, 1826) were not observed in Piketberg. Herbivore species were the most frequently encountered guild across both areas; more herbivores were encountered in the Cederberg (n = 13) than in Piketberg (n = 11). Main leopard prey species were all accounted for in both communities.

Across all guilds, trap rates (RAI) for species detected were generally higher in Piketberg (Figure 3 & Table S2). Noteworthy exceptions include hyrax (Cederberg: 4.05; Piketberg: 3.16), klipspringer (Cederberg: 3.56; Piketberg: 2.41), and rhebok (Cederberg: 0.84; Piketberg: 0.14). A marked difference was the higher RAIs of all carnivores > 4 kg - including leopard (Cederberg: 3.52; Piketberg: 4.65) - as well as most medium (> 0.5 kg and < 100 kg) herbivores, in the transformed Piketberg region (Figure 3 & Table S2). Baboons were the most frequently detected species across both communities (Cederberg: 608 events; Piketberg: 592 events), followed by hyrax in the Cederberg (410 events) and porcupine in Piketberg (540 events). No single species dominated (i.e. > 50% of total trap rates) in any of the two communities.

[Insert Figure 3 here]

High levels of similarity between the two study regions are shown by the Jaccard's Index ($J$ = 0.73) and Sørensen's Coefficient ($CC$ = 0.85). The Jaccard's Index suggests that 73% similarity exists between the contrasting communities. Similarly, the Sørensen Coefficient suggests that the ecological distance is only 15%, supporting close relatedness of ecological make-up in each community.

*Occupancy*

Camera-trap stations were excluded from occupancy analyses when cameras were operational for < 80% of occasions (see Figure 1). Baboon and rhebok were excluded due to insufficient model fit (Table S3). Only strong relationships with space-use and detection probabilities are discussed (see Table 1). Factors that strongly influenced spatial dynamics of leopard and their main prey species in the Cederberg were primarily environmental (56%), whereas anthropogenic (32%) and biotic variables (12%) played a less significant role (Table 1). In contrast, anthropogenic variables (41%) dominated in Piketberg compared to strong influences by environmental (23%) and biotic (36%) factors (Table 1).

[Insert Table 1 here]

*Leopard*

Leopards occurred across the landscape in both communities and were detected at 55 camera-trap stations in Piketberg and 60 stations in the Cederberg, providing naïve occupancy estimates of 0.852 (Piketberg) and 0.833 (Cederberg) respectively. The spatial dynamics of leopards differed between the Cederberg and Piketberg, except for both leopard populations preferring to utilise areas further away from human habitations (Table 1; Figures 4A & 5A). In the Cederberg, leopards also preferred areas in closer proximity to permanent rather than seasonal water sources (Table 1; Figure 4B) but were more likely to be detected further away from water (Table 1; Figure 4E). Furthermore, leopards of the Cederberg were generally less likely to be detected in areas where sympatric meso-carnivores were more abundant (Table 1; Figure 4C) and at higher altitudes (Table 1; Figure 4D). In Piketberg, leopards were less likely to be detected when present at sites characterised by Sandveld vegetation and in areas utilised for grazing, as was indicated by the presence of signs of livestock (Table 1; Figures 5B & C).

[Insert Figure 4 here]

[Insert Figure 5 here]

*Main prey species*

The space-use of grysbok, hyrax, klipspringer, and porcupine were influenced by slightly different factors in the Cederberg and Piketberg (Table 1). None of the variables we considered were found to strongly influence duiker space-use (Table 1). In the primarily protected Cederberg, grysbok preferred areas further away from roads (Table 1), porcupine preferred areas of older vegetation (Table 1), while hyrax preferred areas of Karoo vegetation and seemingly avoided areas where caracal and black-backed jackal were abundant (Table 1). In the agriculturally transformed Piketberg, hyrax, as well as klipspringer, also avoided areas where caracal (black-backed jackal are absent) were prevalent (Table 1). Interestingly, porcupine in Piketberg appeared to prefer areas with greater caracal presence (Table 1).

Various combinations of factors affected the detection probability of these prey species in the Cederberg and Piketberg (Table 1). In both the Cederberg and Piketberg, grysbok were more

likely to be detected if present in areas closer to roads. In Piketberg, detectability of klipspringer was also higher nearer to roads, as was the case for duiker. In the Cederberg, the detection probability of porcupine near roads was also greater. In contrast, the detectability of hyrax in the Cederberg increased further away from roads. Duiker were more likely to be detected closer to human habitations in both the Cederberg and Piketberg, as was grysbok in Piketberg. Oppositely, porcupine in Piketberg were less likely to be detected closer to human habitations. These porcupine were however more likely to be detected in areas that showed evidence of anthropogenic disturbance. In the Cederberg, grysbok were more likely to be detected in areas that experienced anthropogenic disturbance, but klipspringer experienced an opposite effect. In Piketberg, detectability of klipspringer was higher closer to water, particularly permanent water sources. In comparison, duiker in the Cederberg were more likely to be detected further away from water. In Piketberg, duiker and hyrax were both less likely to be detected in areas where leopard RAI was greater. In contrast, grysbok in this region had an opposite relationship and were more likely to be detected where leopards were more prevalent. Interestingly, the relative abundance of leopards played a role in the detection of prey species in Piketberg only. Contrary to their relationship with leopards, hyrax in Piketberg were more likely to be detected in areas where caracal (meso-carnivore) were more abundant. Furthermore, klipspringer were less likely to be detected in both regions in areas where meso-carnivore RAI was higher. Considering the role of vegetation, klipspringer and hyrax in the Cederberg were more likely to be detected in Karoo vegetation, but grysbok and porcupine less so. Porcupine in the Cederberg were also less likely to be detected in older vegetation, as was duiker. Lastly, the detection probability of duiker in both regions were higher at lower altitudes. The same relationship was observed for hyrax in the Cederberg, and the opposite for grysbok in Piketberg.

# Discussion

### Prevalence of leopards

Contrary to expectations, our results, in terms of both relative abundance indices (RAI: Cederberg: 3.52; Piketberg: 4.65) and naïve occupancy ($\psi_{naïve}$: Cederberg: 0.833; Piketberg: 0.852), suggest that leopards are at least equally abundant, or possibly even slightly more abundant, across the agriculturally transformed Piketberg landscape than they are in the primarily protected Cederberg region. A similar observation was made for all carnivores > 4 kg shared between the two communities (Figure 3 & Table S2). Assuming comparable average activity levels, leopards of Piketberg are therefore likely occupying either smaller (i.e. greater density; Snider et al., 2021) or more overlapping home ranges than leopards found in the Cederberg (refer to Müller et al., 2022b). Greater predator abundance can only be sustained by a greater relative carrying capacity (i.e. prey availability), and currently, prey populations in Piketberg appear sufficient to facilitate and sustain relatively larger, potentially denser, and at least equally successful predator populations to those found in the Cederberg. This conclusion is further supported, also contrary to expectation, by higher RAIs in Piketberg compared to the

Cederberg for most medium sized (> 0.5 kg and < 100 kg) herbivores (Figure 3 & Table S2). Differences observed in the abundances of main leopard prey species between the two study regions (Table S2) suggest that leopard diet composition differs (based on prey availability), and that leopards may have had to adapt to a different diet in order to persist in Piketberg.

The main prey species considered in our study are known to comprise approximately 85% of the biomass consumed by leopards in the Cederberg (Müller et al., 2022a), while in other areas of the Western Cape they comprise as much as 91% (Boland) and as little as 57% (Little Karoo) of leopard diets (Mann et al., 2019). Leopards in the Cederberg appear heavily reliant on hyrax and klipspringer in particular, which together made up 61% of biomass consumed (Martins et al., 2010; Müller et al., 2022a). Despite lower abundances recorded for both these prey species in Piketberg relative to the Cederberg during our study (Table S2), the leopard population in Piketberg appeared unaffected. Our findings thus suggest the persistence of leopards in an agriculturally transformed region, highlighting the adaptability, but also the potential vulnerability, of these large apex predators. In the Soutpansberg and Waterberg mountains (Limpopo Province) of South Africa, leopards have also been shown to thrive outside of protected areas (Chase Grey, Kent & Hill, 2013; Swanepoel, Somers & Dalerum, 2015), as is the case across a densely populated agricultural landscape in India (Athreya et al., 2013). Diet composition of leopards in Piketberg is unknown, but our results suggest that these leopards are likely to be less reliant on hyrax and klipspringer than in the Cederberg.

**Natural prey species availability**

Our camera surveys appear to have recorded almost all natural potential prey species (mammals > 0.5 kg) present, as the number of species captured was very close or equal to the total number estimated in both communities. Community composition of potential prey species did differ, but niche composition remained relatively intact across both regions, and each supports complete communities of carnivores and herbivores (Figure 3). Generally, carnivores do not play a significant role in leopard diet in the Western Cape (Martins et al., 2010; Drouilly, Nattrass & O'Riain, 2018; Mann et al., 2019; Müller et al., 2022a), although elsewhere small carnivores are commonly killed (Palomares & Caro, 1999; Hayward et al., 2006). Herbivores unique to each community were all large antelope species (> 100 kg) which are also not of great importance in leopard diet in most of the Western Cape (Martins et al., 2010; Drouilly, Nattrass & O'Riain, 2018; Mann et al., 2019; Müller et al., 2022a), except in the Little Karoo, where their marked presence in leopard diet is attributed to game farming (Mann et al., 2019). The very low abundances and limited distributions (detected at only one station each) of the large antelopes re-introduced on private land in Piketberg (Table S2), are however unlikely to explain why leopards in Piketberg are able to flourish. Ultimately, such predation will also result in farmer-predator conflict and consequently place leopards at risk (Constant, Bell & Hill, 2015). Hence, the minor differences in potential prey species composition and richness we observed between the two communities are unlikely to substantially affect leopard diet.

**Variance of main prey species**

Leopards in Piketberg are more likely to rely on other (than hyrax or klipsringer) main prey species, based on the observed differences in their perceived availability (i.e. RAI; Table S2) in each community. Due to the inability to model probabilities of space-use and detection for baboon and rhebok, we did not speculate on probable causes for differences in their RAIs. It should also be noted that our results for hyrax may be unintentionally skewed because of their restricted habitat (being confined to rocky outcrops; Skinner & Chimimba, 2005) not accounted for in camera set-up procedures, and therefore we suggest caution in interpretation thereof.

In essence, our spatial modelling suggests that anthropogenic factors were generally more likely to affect the behaviour of preferred main prey species of the Cederberg (i.e. hyrax and klipspringer) in a negative manner, and to facilitate alternative main prey species (duiker, grysbok, and porcupine). Factors accompanying agricultural practices (i.e. roads, disturbances, habitations) showed strong correlations across all species, as did environmental factors. Vegetation played a role only in the Cederberg, seemingly facilitating the presence of hyrax and klipspringer in this region (Birss et al., 2016; Visser & Wimberger, 2016). In general, vegetation in Piketberg is denser than across the Cederberg, and thus catered for grysbok and porcupine in particular (Bragg & Child, 2016; Palmer et al., 2016). The top-down influence of predators largely affected hyrax (particularly favoured as prey in the Cederberg by leopard and caracal; Müller et al., 2022a) and klipspringer, and both species seemingly avoided areas heavily utilised by caracal and black-backed jackal (meso-predators) in both communities (resulting in an indirect overlap with leopards in the Cederberg; Müller et al., 2022a). Caracal in Piketberg also seemed to choose areas of greater hyrax activity. Porcupine, which co-exists with caracal in Piketberg, does not generally feature in caracal diet (Müller et al., 2022a). Leopards (apex predator) exhibited direct overlap with grysbok in Piketberg and we would thus expect relatively higher levels of leopard predation on grysbok in this region. In contrast, hyrax and duiker were less active in areas where leopards were more abundant, further suggesting that hyrax do not play a prominent role in leopard diet in Piketberg. However, we cannot disregard the possibility that hyrax, which is a highly preferred leopard prey species (Hayward et al., 2006), may in fact experience very significant predation pressure and therefore their numbers and activity may appear relatively limited in areas shared more frequently with leopards (Wittmer, Sinclair & Mclellan, 2005).

Our findings thus suggest that a combination of anthropogenic, environmental, and biotic factors influences prey species evenness and behaviour, and consequently prey availability. The greater perceived abundance of duiker, grysbok, and porcupine in the agriculturally transformed region may also be facilitated by a preference for readily available crop food resources (these prey species, as well as baboon, are known to frequent the fringes of agricultural land where there is suitable habitat in close proximity: Birss, Relton & Selier, 2016; Bragg & Child, 2016; Palmer et al., 2016) which in turn facilitate leopards in this region. Aside from alternative main prey

species (i.e. grysbok and porcupine) playing an important role in Piketberg, unnatural prey (i.e. livestock or domestic species) might also supplement leopard diet.

**Livestock – An alternative food source?**

In a national park in Pakistan and a human-dominated landscape in India, leopards are almost completely dependent on livestock and other domestic species as prey (Shehzad et al., 2015; Athreya et al., 2016). Our decision to exclude livestock and other domestic species from abundance analyses was because the vastly greater use of livestock proof fences in the Piketberg region prevented accurate and comparable detection of livestock at camera-trap stations. While fences do not prevent the movement of leopards across a landscape, the energetic costs to leopards that accompany their presence may be a driving factor for the killing of more livestock (Wilmers et al., 2017). Müller et al. (2022a) showed that 7% biomass of leopard diet in the Cederberg was comprised of livestock. We believe a greater proportion can be expected in Piketberg, which is supported by the higher levels of confirmed livestock predation events reported in recent years, especially during winter (C. Luyt, 2020, Community Outreach Officer - Cape Leopard Trust, unpublished data; Müller et al., 2022b). Although not found to be of great importance, the inverse relationship between space-use by leopards and presence of livestock in the two contrasting study regions (Table 1), is noteworthy. Leopards in the Cederberg tended to avoid areas with livestock, while in Piketberg they appear to have shown a greater preference for areas with livestock. These results suggest a plausible tendency for greater reliance on livestock by leopards in Piketberg. In the Cederberg, livestock roam more freely but tend to be guarded by herders, whereas in Piketberg they are generally fenced and unguarded. Unguarded, fenced livestock that are not completely predator-proofed may result in leopards being attracted to livestock as prey, especially when natural main prey abundances are low (Odden, Nilsen & Linnell, 2013; Khorozyan et al., 2015). This may subsequently result in an increase in illegal retaliatory killings and make leopards in Piketberg particularly vulnerable (Inskip & Zimmerman, 2009; Soofi et al., 2022).

If livestock serve as regular prey, this has the potential to result in less pressure and reduced ecological regulation of natural prey species, regarded as agricultural pests (G. Malherbe, 2021, Off-reserve Conservation Manager - CapeNature, unpublished damage causing animals database). Examples of this has also been described with other apex predators like snow leopards (*Panthera uncia*, Schreber, 1775) in Nepal and dingoes (*Canis lupis dingo,* Meyer, 1793) in Australia (Johnson & Wallach, 2016; Shrestha, Aihartza & Kindlmann, 2021). Leopards that are less reliant on livestock as prey, provided sufficient preventative measures for livestock predation are employed, will partially limit population explosions of their natural prey species (O'Bryan et al., 2018). Effective preventative mitigation of conflict with crop pests (i.e. prey) will also cater for leopards, offering sufficient natural prey availability in the future which may minimise livestock losses (Odden, Nilsen & Linnell, 2013; Khorozyan et al., 2015). Hence, leopards and their prey species can be regarded as assets on a landscape scale, and pro-active

(preventative and non-lethal) measures employed together by livestock and crop farmers in a community can thus benefit them both instead of either one indirectly inducing conflict for the other. We therefore agree with Du Toit, Cross & Valeix (2017) that a shift in attitude towards asset management, rather than problem control by means of retaliatory killings, will be advantageous. The removal of conflict-prone species would instead be counter-productive for the community (Conradie & Piesse, 2013; Lennox et al., 2018).

**Impacts on leopard behaviour**

Besides potential for retaliatory killings, further direct impacts of agriculture on leopards were evident across both study regions as they avoided areas close to human habitations (Table 1; Figures 4A & 5A). This suggests species sensitivity and echoes the loss of suitable leopard habitat by anthropogenic landscape transformation (Swanepoel et al., 2013; Jacobson et al., 2016). Interestingly, the availability of natural main prey species did not directly dictate spatial utilisation by leopards, probably because leopards (and natural prey) still occurred widely across the study area. However, we found the direct impact of anthropogenic variables on the behaviour of various main prey species to be greater in Piketberg; these have the potential to indirectly affect leopards. Environmental factors that influenced the spatial dynamics of leopards differed between the two regions (Table 1). Greater detectability further away from water in the Cederberg, where sources are presumably more limited, can be explained since leopards are largely independent of water (Bothma, 2005). Leopards in this region did however show a preference for areas closer to permanent (e.g. rivers; Table S1) rather than seasonal (e.g. streams; Table S1) water sources, but this is likely to be a simple consequence of these water sources being dry and unusable at the time. The lower detection probability of leopards in Sandveld vegetation and areas presumably used for grazing in Piketberg indicate that fine-scale habitat utilisation by leopards is likely to be selective and affected by agricultural activities. The influence of altitude observed in the Cederberg is assumed to be a consequence of the slightly higher density recorded for leopards in the region during the summer months, which relates to individuals occupying smaller home ranges on the more accessible lower mountain slopes at this time of year (Müller et al., 2022b). Finally, the relationship we observed between leopards and meso-carnivores in the Cederberg is consistent with the conclusions of Müller et al. (2022a): Caracal (meso-predator) tends to avoid leopards (apex predator) in time and space.

**Study limitations**

Potential criticisms of our study are that data were collected roughly two years apart, and that it investigated factors influencing behaviour only at a single spatial scale. We are aware that community structure could be influenced by weather on a seasonal or annual basis. The Western Cape experienced a relatively dry year (South African Weather Service, 2021) prior to the Cederberg survey and recorded precipitation of 212.9 mm below the annual mean (2017; Data provided by www.meteoblue.com) in the region. A precipitation anomaly of 139.9 mm below

the mean (2019; Data provided by www.meteoblue.com) was also noted prior to the survey in the Piketberg region. Ideally, ecological modelling should aim to incorporate different orders of scale (e.g. Pitman et al., 2017), but this is not always practical. We concur that spatial scale must, however, be accounted for in conservation decision-making (also see McManus et al., 2021). Our results can be used to inform and support conservation policies that aim to cater for free-roaming leopards in human-altered landscapes.

## Conclusions

No real differences were apparent between the potential prey species composition or richness, or the abundance of leopards, in the agriculturally transformed Piketberg and the primarily protected Cederberg regions. Our results, therefore, suggest that transformed regions have the potential to facilitate biological diversity, including apex predators (see Linell, Swenson & Anderson, 2001). The main prey species of leopards in the Cederberg were, however, relatively less abundant in Piketberg, but this difference was not reflected in the respective leopard populations. We believe that greater utilisation of alternative main prey species to those preferred in the Cederberg, likely including livestock, facilitates persistence of the Piketberg leopard population, and that this is a probable driving factor of high levels of human-wildlife conflict. Our findings also suggest that a variety of ecological factors strongly influenced the spatial dynamics and behaviour of leopards and their main prey species in a complex manner, but anthropogenic factors played a relatively larger role in the agriculturally transformed region (also see Rogan et al., 2022). We argue that a multi land-use, multi-species (predator and prey), and pro-active (non-lethal) management approach, that encourages co-existence and aims to limit the cascade of ecosystem effects that could follow human-induced changes to the landscape, can benefit both livestock and crop farmers. Ultimately, such a collaborative and holistic approach can provide incentive to conserve apex predators and their prey and is therefore required to ensure the conservation of apex predators on working lands worldwide. We also encourage further detailed investigation of the leopard population in Piketberg, including density, home-range, population structure, dietary and human-wildlife (both leopards and their prey) conflict analyses, to further inform local conservation management decision-making and maintain its leopard population going forward.

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## Figure legends

**Figure 1:** Maps showing the location of the Western Cape province within South Africa (a), and the proximity of the survey areas within the Western Cape (b). Main map shows the location of camera-trap stations for both Cederberg and Piketberg. Failed camera-trap stations (because of major camera malfunctioning, fire, other damage, or theft) are noted. Formally proclaimed protected areas (CapeNature reserves) are also highlighted.

**Figure 2:** Rarefied species accumulation curves for medium-to-large (> 0.5 kg) terrestrial mammals (i.e. potential leopard prey species) photographed in the primarily protected Cederberg and agriculturally transformed Piketberg regions. Both curves approach an asymptote, indicating sufficient sampling effort.

**Figure 3:** Distribution of medium-to-large (> 0.5 kg) terrestrial mammals (i.e. potential leopard prey species) in the Cederberg and Piketberg on the basis of body size and trophic category. Each circle represents a species in functional space. The size of the circle is proportional to the trapping rate (RAI) for that species.

**Table 1:** QAICc weights ($w$) for covariates from well-supported models ($w$ > 0.10 and QAICc < 2) for each species (leopard + main prey) in each community. Either the direction of the relationship for covariates from the best fit models or the parameter probability estimate (± standard deviation) for top models are indicated in parentheses.

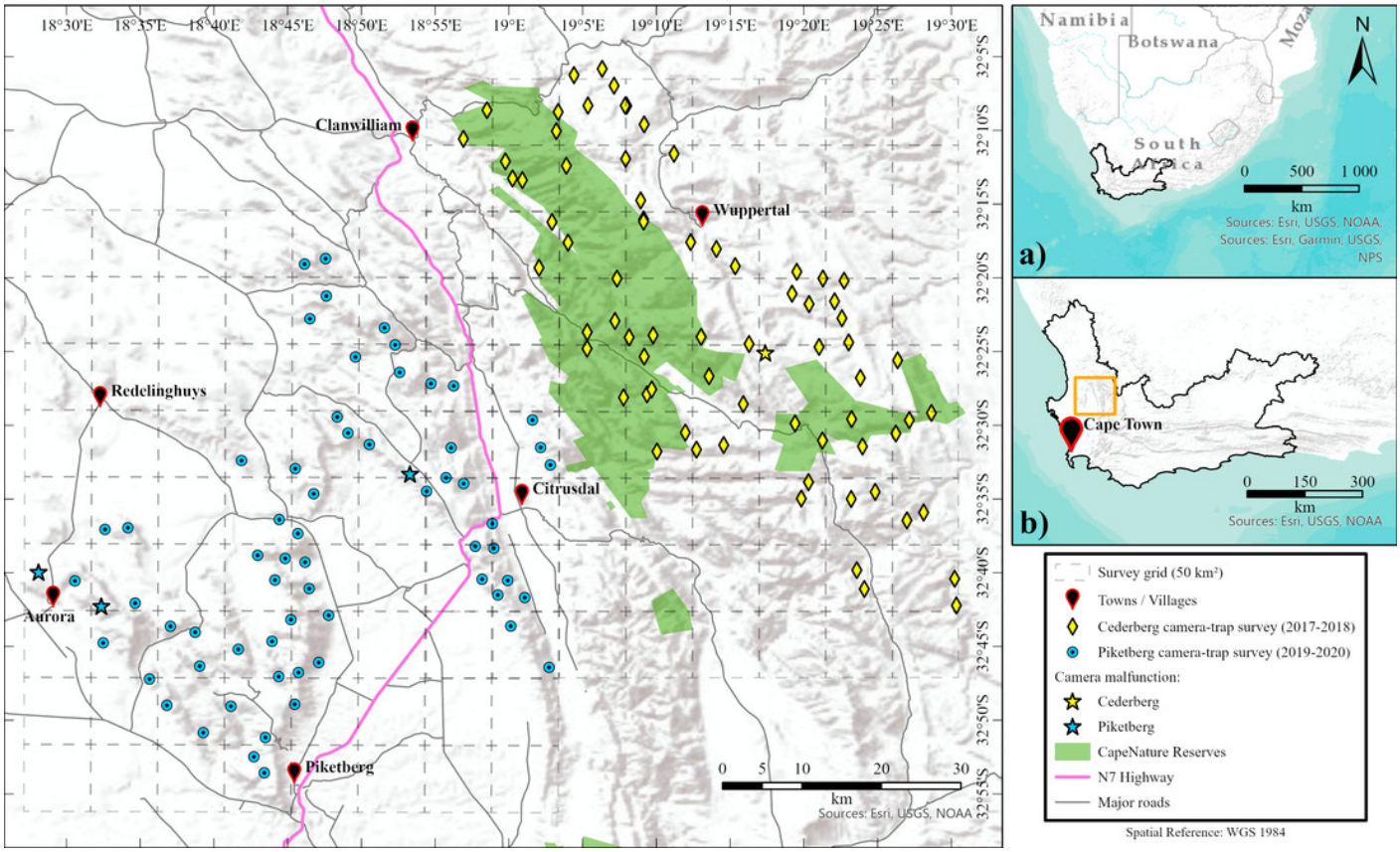
**Figure 4:** Detection and space-use (i.e. occupancy) probabilities for leopards with regards to variables with strong associations in the Cederberg.

**Figure 5:** Detection and space-use (i.e. occupancy) probabilities for leopards with regards to variables with strong associations in Piketberg. Values in graphs B and C are the detection probabilities for leopards across the various habitat types in areas without (B) and with (C) livestock signs present.

# Figure 1

Location of survey regions.

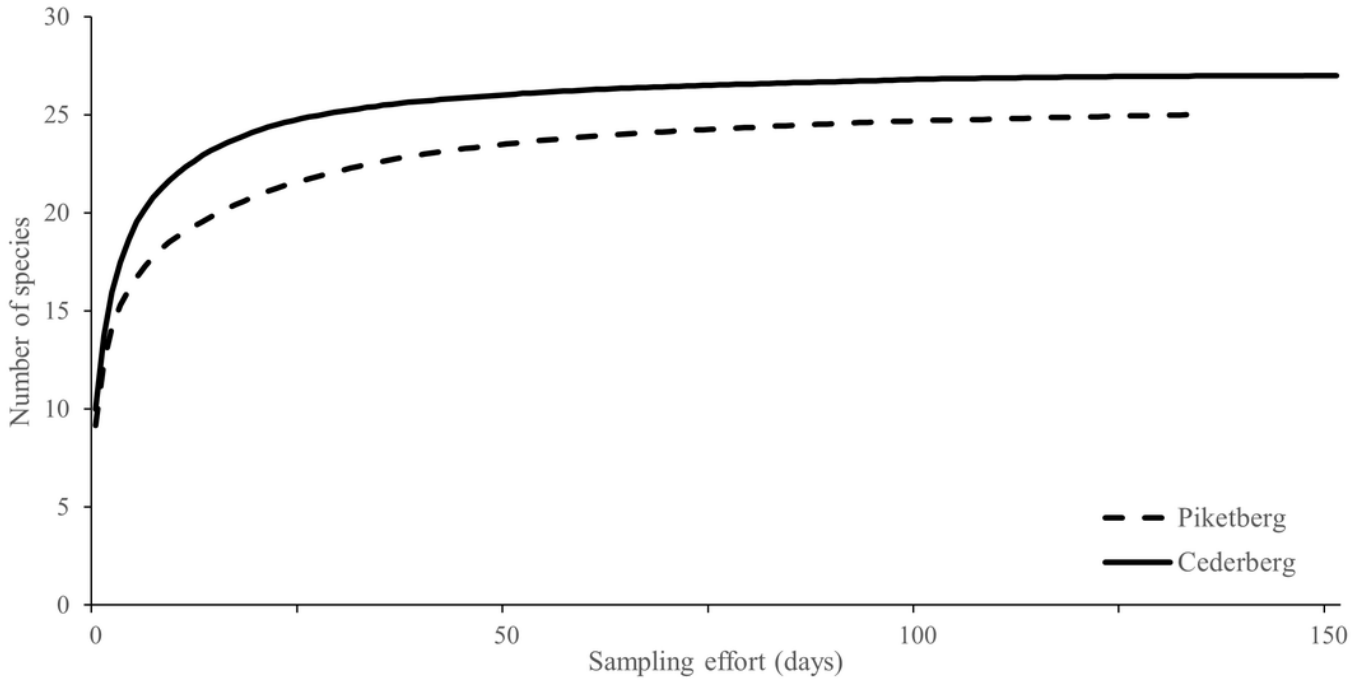
Maps showing the location of the Western Cape province within South Africa (a), and the proximity of the survey areas within the Western Cape (b). Main map shows the location of camera-trap stations for both Cederberg and Piketberg. Failed camera-trap stations (because of major camera malfunctioning, fire, other damage, or theft) are noted. Formally proclaimed protected areas (i.e. CapeNature reserves) are also highlighted.



# Figure 2

Rarefied species accumulation curves for medium-to-large (> 0.5 kg) terrestrial mammals (i.e. potential leopard prey species) photographed in the Cederberg and Piketberg regions.

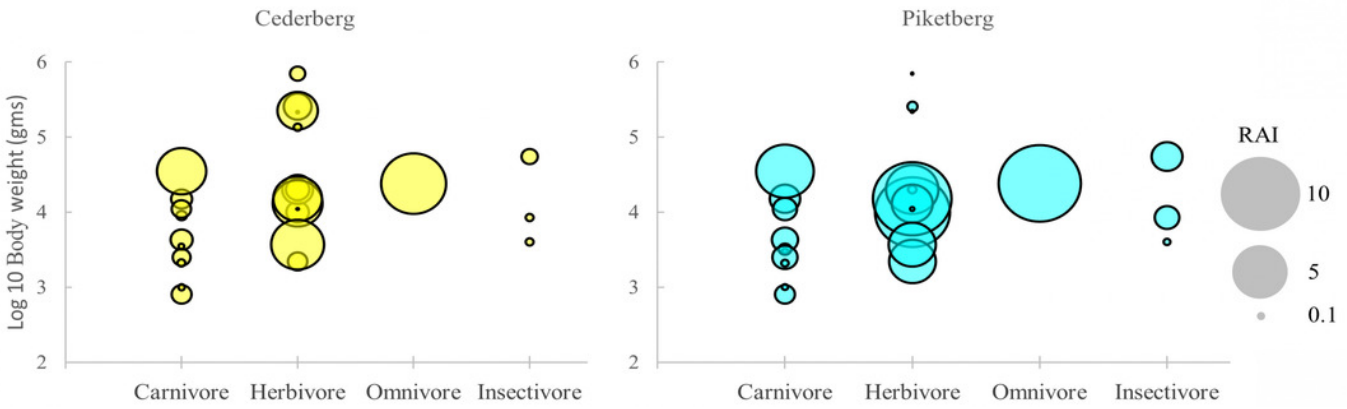
Both curves approach an asymptote, indicating sufficient sampling effort.



# Figure 3

Distribution of medium-to-large (> 0.5 kg) terrestrial mammals (i.e. potential leopard prey species) in the Cederberg and Piketberg on the basis of body size and trophic category.

Each circle represents a species in functional space. The size of the circle is proportional to the trapping rate (RAI) for that species.



## Table 1(on next page)

QAICc weights (*w*) for covariates from well-supported models ($w > 0.10$ and QAICc < 2) for each species (leopard + main prey) in each community.

Either the direction of the relationship for covariates from the best fit models or the parameter probability estimate (± standard deviation) for top models are indicated in parentheses.

| Species | Parameter | Covariate | Cederberg | Piketberg |
|---|---|---|---|---|
| **Leopard** | Ψ | habitation | 0.49 (+)* | 0.12 (+)* |
| | | water source (seasonal) | 0.49 (-)* | 0.14 (+)[a] |
| | | prey | 0.49 (-)[a] | |
| | | livestock (yes) | 0.28 (-)[a] | 0.14 (+)[b] |
| | | altitude | | 0.26 (-)[a] |
| | | null | | 0.33 (0.92 ± 0.04) |
| | *p* | carnivores | 0.49 (-)* | |
| | | altitude | 0.49 (-)* | |
| | | water | 0.49 (+)* | |
| | | prey | 0.49 (+)[a] | |
| | | vegetation (Renoster) | | 0.33 (-)[a] |
| | | vegetation (Riverine thicket) | | 0.33 (+)[b] |
| | | vegetation (Sandveld) | | 0.33 (-)* |
| | | livestock (yes) | | 0.33 (-)* |
| **Duiker** | Ψ | road | 0.72 (-)[a] | |
| | | altitude | 0.72 (+)[a] | |
| | | carnivores | 0.28 (+)[a] | |
| | | water source (seasonal) | 0.28 (-)[a] | |
| | | caracal | | 0.17 (+)[a] |
| | | water | | 0.13 (+)[a] |
| | | disturbance (yes) | | 0.10 (+)[a] |
| | | vegetation (Renoster) | | 0.10 (-)[a] |
| | | vegetation (Riverine thicket) | | 0.10 (-)[a] |
| | | vegetation (Sandveld) | | 0.10 (+)[a] |
| | | null | | 0.22 (0.55 ± 0.08) |
| | *p* | altitude | 0.72 (-)* | 0.22 (-)* |
| | | leopard | 0.72 (+)[a] | 0.22 (-)* |
| | | water | 0.72 (+)* | |
| | | vegetation age | 0.72 (-)* | |
| | | vegetation (Karoo) | 0.72 (-)[a] | |
| | | habitation | 0.72 (-)* | 0.22 (-)* |
| | | road | 0.72 (-)[a] | 0.22 (-)* |
| **Grysbok** | Ψ | road | 0.16 (+)* | |
| | | leopard | 0.16 (+)[a] | 0.18 (+)[a] |
| | | water source (seasonal) | 0.16 (-)[a] | |
| | | altitude | | 0.37 (+)[a] |
| | | disturbance (yes) | | 0.15 (-)[a] |
| | | vegetation (Karoo) | 0.11 (+)[a] | |
| | | null | | 0.30 |
| | *p* | vegetation (Karoo) | 0.16 (-)* | |
| | | road | 0.16 (-)* | 0.37 (-)* |
| | | disturbance (yes) | 0.16 (+)* | |
| | | leopard | | 0.37 (+)* |
| | | altitude | | 0.37 (+)* |
| | | habitation | | 0.37 (-)* |
| **Hyrax** | Ψ | vegetation (Karoo) | 0.36 (+)* | |

| | | | | |
|---|---|---|---|---|
| | | carnivores | 0.36 (-)* | |
| | | water | 0.27 (+)[a] | |
| | | leopard | 0.22 (+)[a] | 0.24 (+)[a] |
| | | disturbance (yes) | 0.15 (-)[a] | |
| | | caracal | | 0.37 (-)* |
| | | habitation | | 0.24 (+)[a] |
| | *p* | vegetation (Karoo) | 0.36 (+)* | |
| | | road | 0.36 (+)* | |
| | | altitude | 0.36 (-)* | |
| | | carnivores | 0.36 (-)[a] | |
| | | leopard | | 0.37 (-)* |
| | | caracal | | 0.37 (+)* |
| **Klipspringer** | Ψ | altitude | 0.32 (+)[a] | |
| | | water source (seasonal) | 0.32 (+)[a] | |
| | | livestock (yes) | 0.15 (+)[a] | |
| | | caracal | | 0.17 (-)* |
| | | water | | 0.12 (+)[a] |
| | | disturbance | | |
| | | leopard | | 0.17 (-)[a] |
| | *p* | vegetation (Karoo) | 0.32 (+)* | |
| | | carnivores | 0.32 (-)* | |
| | | disturbance (yes) | 0.32 (-)* | |
| | | water source (seasonal) | | 0.17 (-)* |
| | | water | | 0.17 (-)* |
| | | road | | 0.17 (-)* |
| | | caracal | | 0.17 (-)* |
| **Porcupine** | Ψ | caracal | | 0.38 (+)* |
| | | road | | 0.31 (-)[a] |
| | | disturbance (yes) | | 0.30 (+)[a] |
| | | vegetation age | 0.38 (+)* | |
| | | water | 0.38 (+)[a] | |
| | | leopard | 0.18 (-)[a] | |
| | *p* | habitation | | 0.38 (+)* |
| | | disturbance (yes) | | 0.38 (+)* |
| | | altitude | | 0.38 (+)[a] |
| | | vegetation (Karoo) | 0.38 (-)* | |
| | | vegetation age | 0.38 (-)* | |
| | | road | 0.38 (-)* | |
| | | carnivores | 0.38 (+)[a] | |

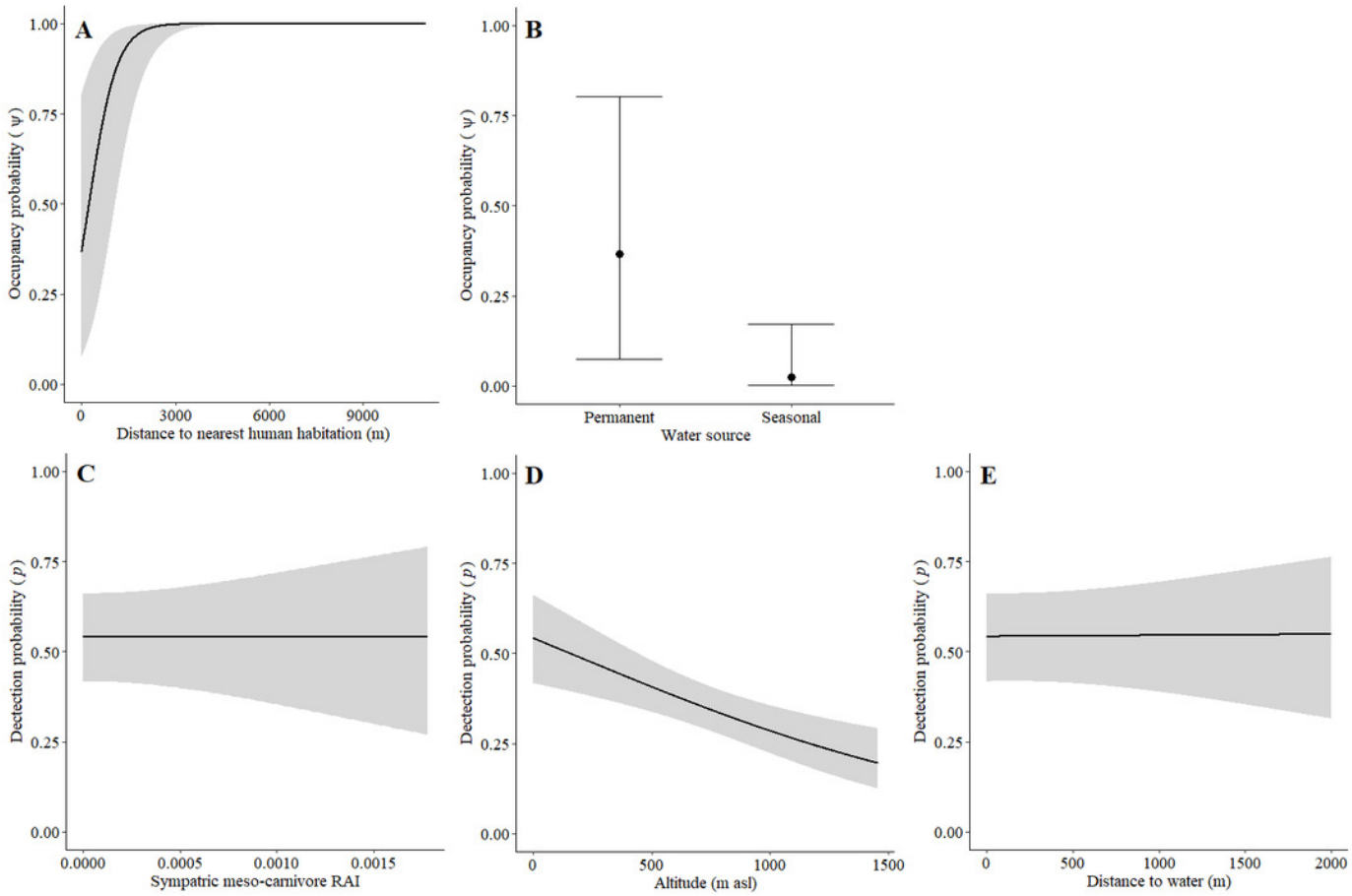
*strong evidence of relationship (CI estimates do not overlap 0)

[a] medium evidence of relationship (CI estimates overlap 0, but are not centred on 0)

[b] weak evidence of relationship (CI estimates overlap 0 and are centred on 0)

# Figure 4

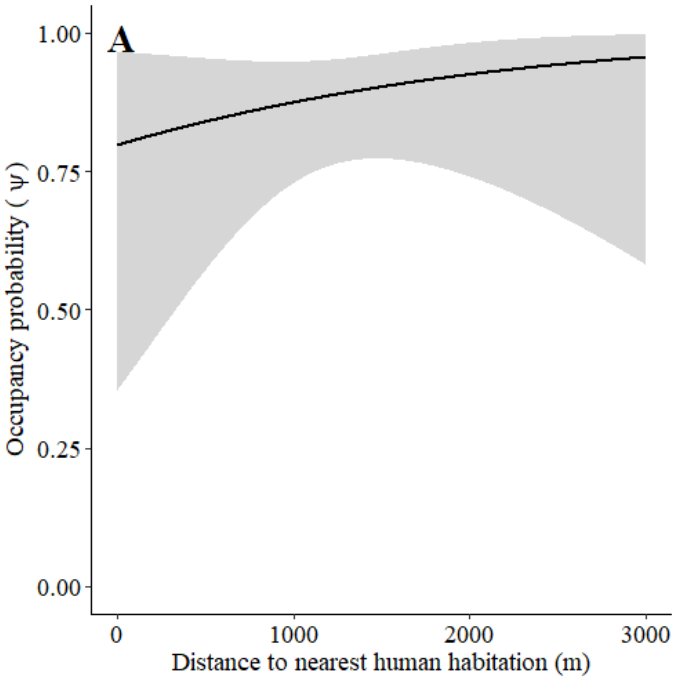
Detection and space-use (i.e. occupancy) probabilities for leopards with regards to variables with strong associations in the Cederberg.

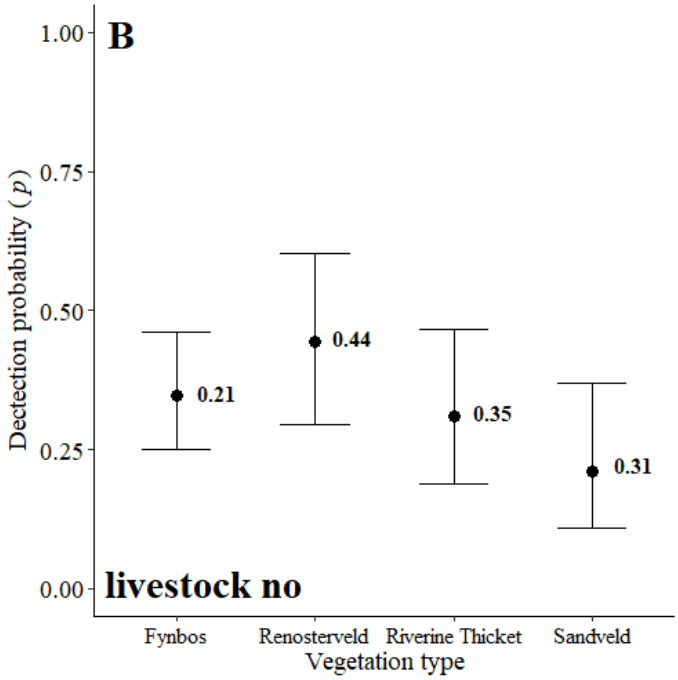


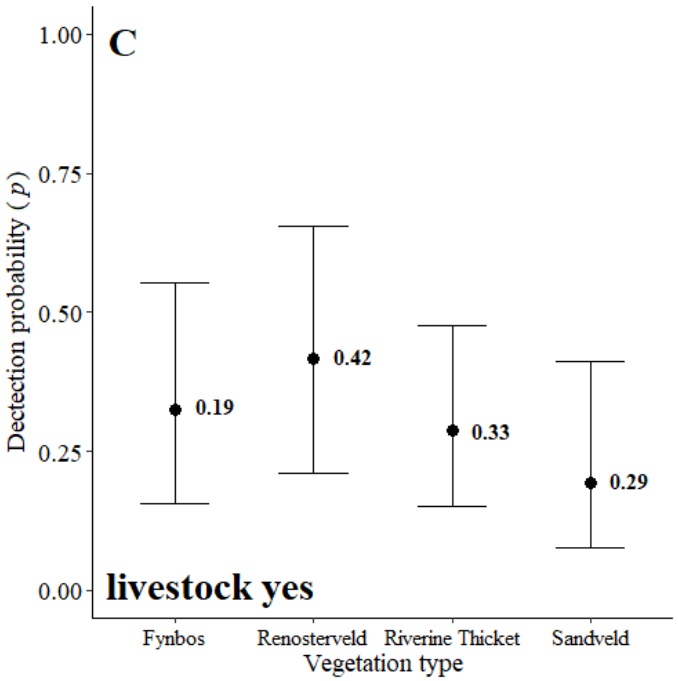
# Figure 5

Detection and space-use (i.e. occupancy) probabilities for leopards with regards to variables with strong associations in Piketberg.

Values in graphs B and C are the detection probabilities for leopards across the various habitat types in areas without (B) and with (C) livestock signs present.


A
1.00
0.75
0.50
0.25
0.00
Occupancy probability ( ψ)
0
1000
2000
3000
Distance to nearest human habitation (m)


B
1.00
0.75
0.50
0.25
0.00
Dectection probability ( p)
0.21
0.44
0.35
0.31
livestock no
Fynbos
Renosterveld
Riverine Thicket
Sandveld
Vegetation type


C
1.00
0.75
0.50
0.25
0.00
Dectection probability ( p)
0.19
0.42
0.33
0.29
livestock yes
Fynbos
Renosterveld
Riverine Thicket
Sandveld
Vegetation type