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
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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 maintain 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 multitude of threats attributable to competition for space and resources with humans. Using camera-trap data, we 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 indicate prey availability in each region. Factors influencing spatial utilisation by 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), supported by both the Jaccard's Index (J = 0.73) and Sørensen's Coefficient (CC = 0.85), suggested high levels of similarity across the two regions. Main leopard prey species were present in both regions, but their relative abundances differed. Grey rhebok, klipspringer, and rock hyrax were more abundant in the Cederberg, while Cape grysbok, Cape porcupine, chacma baboon, and common duiker were more abundant in Piketberg. Leopards persisted across the agriculturally transformed landscape despite these 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 greater 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 mammalian diversity, including apex predators. We iterate that conservation measures for 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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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 maintain 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 multitude of threats attributable to competition for space and resources with humans. Using camera-trap data, we 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 indicate prey availability in each region. Factors influencing spatial utilisation by 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), supported by both the Jaccard's Index (J = 0.73) and Sørensen's Coefficient (CC = 0.85), suggested high levels of similarity across the two regions. Main leopard prey species were present in both regions, but their relative abundances differed. Grey rhebok, klipspringer, and rock hyrax were more abundant in the Cederberg, while Cape grysbok, Cape porcupine, chacma baboon, and common duiker were more abundant in Piketberg. Leopards persisted across the agriculturally transformed landscape despite these 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 greater 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 mammalian diversity, including apex predators. We iterate that conservation measures for 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

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

79 Traditionally, it was believed that vast, relatively intact ecosystems were required to effectively
80 support viable apex predator populations (Sillero-Zubiri & Laurenson, 2001; Morrison et al.,
81 2007). Their high trophic position and large body size suggests that they require extensive home
82 ranges which sustain sufficient prey abundances (Morrison et al., 2007; Ripple et al., 2014).
83 These spatial requirements often bring apex predators into conflict with humans (Inskip &
84 Zimmerman, 2009; Nyhus, 2016) as they are amongst the first species to be affected by the
85 expansion of human populations and associated cultivation of previously untouched habitats
86 (Morrison et al., 2007; Ripple et al., 2014; Aebischer et al., 2020). A species that is influenced by
87 anthropogenic development to an increasing extent across the globe is the leopard (*Panthera*
88 *pardus*; Linnaeus, 1758). Leopards are the most widespread large felid, occurring across much of
89 Africa and tropical Asia (Nowell & Jackson, 1996; Stein et al., 2020). They are very adaptable
90 and successfully occupy a large variety of habitats across their range (Jacobson et al., 2016; Stein
91 et al., 2020), including areas alongside large urban spaces (Kuhn, 2014; Braczkowski et al.,
92 2018). However, their ability to inhabit areas in such close proximity to humans makes them
93 particularly susceptible to competition with humans for space and resources, inevitably placing
94 leopards at great risk.

95 Globally, leopards are considered as Vulnerable as their populations are declining and they face
96 multiple threats to their survival (Stein et al., 2020). An estimated 75% of their historic range has
97 been lost (Jacobson et al., 2016), where the average loss for large carnivore species is only
98 around 53% (Ripple et al., 2014). Although suitable habitat in southern Africa – arguably hosting
99 the healthiest leopard population across the species range (Stein et al., 2020) – remains widely
100 distributed, it is highly fragmented, having experienced ~51% decline since 1750 (Jacobson et

101   al., 2016). Anthropogenic activities, in particular agricultural practices, are primarily deemed
102   responsible for this fragmentation (Swanepoel et al., 2013). Indeed, Brink & Eva (2009) showed
103   that agricultural land increased by 57% at the expense of natural vegetation in sub-Saharan
104   Africa in just 25 years (1975-2000). In South Africa, ~68% of remaining habitat suitable for
105   leopards is found in areas that are naturally susceptible to land-use transformation (Swanepoel et
106   al., 2013). Leopards that occupy these non-protected regions are most at risk of being killed by
107   human-induced causes such as snares, hunts, poison, or motor vehicle collisions (Balme, Slotow
108   & Hunter, 2010; Swanepoel et al., 2013; 2015). Consequently, it is vitally important that
109   conservation measures be established to accommodate free-roaming leopards across transformed
110   landscapes to facilitate functional population connectivity and ensure ecosystem resilience
111   (Balme, Slotow & Hunter, 2010; Swanepoel et al., 2013; Swanepoel, Somers & Dalerum, 2015).
112   Most research on leopards in South Africa has taken place inside protected areas (Balme et al.,
113   2014), which means that inadequate data is likely jeopardizing the conservation of the species on
114   working lands.

115   Free-roaming leopards are the last remaining apex predator found in the Cape Floristic and
116   Succulent Karoo Regions (Martins & Martins, 2006), which are both biodiversity hotspots and
117   together forms the Greater Cape Floristic Region (Born, Linder & Desmet, 2007), in the Western
118   Cape province of South Africa. Here, leopards generally occupy considerably larger home ranges
119   (Patterson, 2008) and occur at much lower densities (Martins & Martins, 2006) than leopards
120   found elsewhere in Africa (excluding the Kgalagadi; Mizutani & Jewell, 1998; Bothma &
121   Bothma, 2012). Furthermore, these leopards are also considered to be smaller on average than
122   most leopards (excluding Arabian leopard; Spalton & Al Hikmani, 2006) found elsewhere
123   throughout the species range (Stuart, 1981; Martins & Martins, 2006). Almost 90% of the total
124   area of the Western Cape is regarded as potential farmland, and the human population of the
125   province ($\pm$55 people per km^2; Statistics South Africa, 2021) has consistently grown at a faster
126   rate than the national average (Partridge, Morokong & Sibulali, 2021). The Western Cape is
127   therefore an ideal location to investigate the influence of landscape transformation, both directly
128   and indirectly, on this apex predator.

129   The aforementioned characteristics of leopards in the Western Cape all presumably reflect
130   adaptation to a different diet (Martins et al., 2010). With a great diversity in habitat usage,
131   leopards opportunistically hunt a wide range of prey, depending on local availability (Hayward et
132   al., 2006). A decline in their primary prey base can, however, impact leopard population
133   structure (Marker & Dickman, 2005; Ray, Hunter & Zigouris 2005; Wolf & Ripple, 2016), and
134   may also affect human-wildlife conflict levels by altering leopard behaviour (Khorozyan et al.,
135   2015). Human-wildlife conflict has long been prevalent in the Western Cape and remains a
136   complex challenge to this day (Martins & Martins, 2006; Nieman, Wilkinson & Leslie, 2020).
137   Indeed, leopards within this region are not only deemed responsible for livestock losses, but
138   direct conflict also exists with leopard prey species, often regarded as crop raiders (G Malherbe –
139   Off-reserve Conservation Manager at CapeNature, 2021, pers. comm.).

140   The primary (main) prey base for leopards across the Western Cape include common duiker
141   (duiker; *Sylvicapra grimmia*, Linnaeus, 1758), Cape grysbok (grysbok; *Raphicerus melanotis*,
142   Thunberg, 1811), klipspringer (*Oreotragus oreotragus*, Zimmermann, 1783), and grey rhebok
143   (rhebok; *Pelea capreolus*, Forster, 1790), as well as rock hyrax (hyrax; *Procavia capensis*,
144   Pallas, 1766), Cape porcupine (porcupine; *Hystrix africaeaustralis*, Peters, 1852), and chacma
145   baboons (baboon; *Papio ursinus*, Kerr, 1792) (Martins et al., 2010; Drouilly, Nattrass & O'Riain,
146   2018; Mann et al., 2019; Müller et al., 2022a). In addition to suffering retaliatory killings, these
147   species are also targeted for the illegal harvesting of bushmeat by means of snaring in the
148   province (Nieman et al., 2019). An akin competitive relationship between humans and leopards
149   has previously been documented in the Congo Basin (Henschel et al., 2011), with profound
150   negative consequences for leopards. Illegal hunting, which impacts prey species availability, is a
151   continuous concern for wildlife worldwide (Lindsey et al., 2013; Heurich et al., 2018). Besides,
152   snares can also be responsible for the direct capture of leopards resulting in severe injury or
153   death (Swanepoel et al., 2015; Williams et al., 2017; Nieman, Leslie & Wilkinson, 2019; Gubbi,
154   Kolekar & Kumara, 2021).

155   As the only terrestrial apex predator to persist in the Western Cape, free-roaming leopards are
156   expected to be sensitive to changes in prey species populations. Yet, little is known about the
157   extent to which this relationship may be influenced by humans in the context of commercial
158   agriculture. Several studies investigating the drivers of leopard occurrence, density, or ranging
159   behaviour (e.g. Jiang et al., 2015; Allen et al., 2020; Searle et al., 2020; Snider et al., 2021;
160   Loveridge et al., 2022), and predator-prey overlap (e.g. Dias, de Campos & Rodrigues, 2018;
161   Havmøller et al., 2020; Palei et al., 2021; Sehgal et al., 2022; Zaman et al., 2022), have been
162   performed worldwide. However, until relatively recently, few studies have investigated African
163   leopard (*P. p. pardus*) ecology in human-disturbed landscapes (see Marker & Dickman, 2005;
164   Williams et al., 2017; Strampelli et al., 2018) – particularly in commercial agricultural regions.
165   Furthermore, limited comparisons of predator populations between analogous protected and non-
166   protected regions have been made (e.g. Swanepoel, Somers & Dalerum, 2015; Drouilly, Nattress
167   & O'Riain, 2018; Curveira-Santos et al., 2020; Faure et al., 2021). Considering that half of all
168   habitable land worldwide is used for agriculture (Ellis et al., 2010; Ritchie & Roser, 2013) –
169   regarded as the biggest driver of terrestrial habitat loss (IPBES, 2019) – our understanding of
170   factors which could best enable (or inhibit) the persistence of apex predators in agriculturally
171   transformed environments, including variables influencing the availability of their natural prey
172   species, is vital to aid management decision making and account for in cost-benefit models that
173   aim to minimise conflict. Inferences about spatial variation in species composition and diversity
174   (richness and evenness; Colwell, 2009) are also important, both to ecological hypotheses about
175   structure and function of communities and to community-level conservation management
176   (Nichols et al., 1998).

177   This study investigated potential prey species diversity, community structure, and factors
178   affecting the spatial behaviour of leopards and their main prey species, in both an agriculturally

179 transformed and a largely protected landscape. First, we aimed to determine whether any real
180 differences exist with reference to potential prey species found in each community and whether
181 any such difference is evidently reflected in the respective leopard subpopulations. Second, we
182 aimed to evaluate and compare drivers of habitat utilisation by leopards and their main prey in
183 each region. We anticipated a greater diversity of potential leopard prey species to exist in the
184 protected community, as well as differences in community structure. Relative leopard and prey
185 abundances were predicted to be lower in the transformed agricultural region, and anthropogenic
186 factors were expected to negatively influence space-use, by leopards as well as their main prey
187 species, across the greater landscape.

Materials & Methods

188

Ethical statement

189

190 Relevant permissions to conduct our research were granted by the Social, Behavioural and
191 Education Research Ethics Committee at Stellenbosch University (Project ID #15315),
192 CapeNature (Permit #CN44-59-12321), and in writing by all landowners involved. Data
193 collection was performed using camera-traps, which is a non-invasive research method. All data,
194 including any images captured of human subjects, were treated as strictly confidential.

Study area

195

196 The Piketberg region (hereafter Piketberg) encompasses a transformed landscape that is
197 primarily characterised by mixed agricultural practices. Our study area is located approximately
198 130 to 160 km north of Cape Town, South Africa, and situated southwest of the Cederberg
199 region (Figure 1). The survey area was approximately 1500 km^2 in size (53 - 864 metres above
200 sea level), covering 55 privately owned mixed agricultural farms extending north from the town
201 of Piketberg to Paleisheuwel, with Citrusdal in the east and Aurora on the western boundary
202 (Figure 1). The area consists of natural vegetation forming a mosaic, highly fragmented by
203 livestock (e.g. cattle (*Bos taurus,* Linnaeus, 1758), horses (*Equus ferus caballus,* Linnaeus,
204 1758), sheep (*Ovis aries,* Linnaeus, 1758), goats (*Capra hircus,* Linnaeus, 1758), pigs (*Sus
205 domesticus,* Erxleben, 1777)), fruit, and other crop farmlands in and around mountainous terrain
206 (Linder, 1976; Mucina & Rutherford, 2006).

207 The Cederberg region (hereafter Cederberg), known for its rugged remoteness, is a largely
208 protected area first proclaimed in 1973 and located 200 to 250 km northeast of Cape Town
209 (Figure 1). This survey area was approximately 1700 km^2 in size (254 - 1455 metres above sea
210 level) and included the Matjiesrivier Nature Reserve and the Cederberg Wilderness Area. Both
211 areas are formally protected and managed by the provincial conservation regulation body and
212 authority in the Western Cape, known as CapeNature (Figure 1). Privately owned areas included
213 were Bushmans Kloof Wilderness Reserve, community owned land used for the harvesting of
214 rooibos and limited pastoralism by subsistence farmers, and the Cederberg Conservancy,

215 consisting of pro-conservation farms that are used for ecotourism and largely kept in a natural
216 ecological state. The two main biomes present are Fynbos and Succulent Karoo in mountainous
217 terrain (Mucina & Rutherford, 2006).

218   [Insert Figure 1 here]

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

227 **Field sampling methods**

228 *Camera-trap surveys*

229 Single season (dry summer – November to March) subsets of photographic data that were
230 collected in the Cederberg (2017-2018) and Piketberg (2019-2020) were used for our study. The
231 73 camera-trap stations (n = 146 cameras) in the Cederberg were all located within areas with
232 protected status, whereas the 64 camera-trap stations (n = 128 cameras) in Piketberg were
233 situated in non-protected areas nestled between and on farmlands (Figure 1). Paired motion and
234 heat detecting Cuddeback X-Change series camera-traps were used at each camera station during
235 both surveys. Our setup procedures followed standard protocols optimised for the detection of
236 leopards, whereby the landscape across both study regions was divided into 50 km^2 blocks
237 (Figure 1), based on the minimum estimated home range size recorded for a female leopard with
238 cubs in the Western Cape (37 km^2; Martins, 2010; also see Müller et al., 2022a; 2022b). Camera-
239 trap stations were dispersed across mountainous habitat with mean distances of 2.78 km
240 (Cederberg) and 3.09 km (Piketberg) between individual stations and two to three stations per
241 block (Figure 1). Camera-trap locations were selected based on the presence of tracks and signs
242 of leopards and their main natural prey species found in the nearby vicinity on initial site
243 investigation. Cameras were mounted ~40 cm above the ground and perpendicular to a game
244 trail, road, or drainage line. Camera-traps were serviced at an interval of roughly eight weeks to
245 download images, change batteries, perform site data collection (i.e. recording covariates around
246 each site), and for general maintenance.

247 *Covariate data*

248 Environmental (i.e. altitude, vegetation type, vegetation age, nearest water source type and its
249 distance) and anthropogenic (i.e. distances to the nearest road and human habitation, evidence of

250   disturbance, livestock, and/or hunting) covariates surrounding each camera-trap station were
251   recorded during each servicing period (see Supplementary Material, Table S1). Some categorical
252   and binomial covariates were determined with a repeated physical site inspection of the
253   surroundings performed by a trained and experienced individual covering a 100 m radius around
254   each station (Table S1). Other variables were determined by a combination of physical
255   investigation, with recordings made using a GPS unit (Garmin ETrex 10), and local knowledge
256   (Table S1). Any further verification was performed using Google Earth (Google, n.d.) and
257   historical fire records (Table S1). The chosen covariates reflect natural and human-induced
258   factors that could influence predator and prey space-use or detection at each site.

259   **Data analyses**

260   *Camera-trap data*

261   Camera Base software (Tobler, 2010) was used to process images and extract meta-image
262   information from each photograph (image name, date, and time) while correcting for any time
263   stamp errors. Faunal species and number of individuals in each photograph was identified where
264   possible. Primary analyses were performed using the Camera Trap Analysis Package (CTAP)
265   software developed by the Zoological Society of London (Amin & Wacher, 2017). Only
266   terrestrial mammals > 0.5 kg, including leopard (see Charsley (1977), Steyn & Funston (2006),
267   and Balme & Hunter (2013) for examples of reported cannibalism), were considered as potential
268   leopard prey species for analyses. They are the main target group for camera-traps set up in this
269   manner and are also generally regarded as the main dietary component of leopards (Hayward et
270   al., 2006; Tobler et al., 2008; Martins et al., 2010; Drouilly, Nattrass & O'Riain, 2018; Mann et
271   al., 2019; Müller et al., 2022a). Relative abundance indices (RAI; i.e. number of events, where
272   an "event" is defined as any image sequence for a given species occurring after an interval of $\geq$
273   60 minutes from a previous sequence of that species, per 100 days of camera trapping; Karanth
274   & Nichols, 1998; Amin et al., 2018) per camera-trap station were calculated for known main
275   prey species of leopards in the study area, sympatric meso-carnivores - caracal (*Caracal caracal*,
276   Schreber, 1776) and black-backed jackal (*Canis mesomelas*, Schreber, 1775) - and leopards, and
277   used as biotic covariates during occupancy modelling (Table S1). Despite being influenced by
278   sampling design or species' behaviour (Sollmann et al., 2013), RAI is still considered a suitable
279   tool for assessing species occurrence (Hedwig et al., 2018; Palmer et al., 2018).

280   *Community structure*

281   Biological communities can differ in species composition, total number of species (richness), and
282   the relative abundance of species (evenness) (Colwell, 2009). Species sample-based rarefaction
283   curves were constructed and the terrestrial medium-to-large (> 0.5 kg) mammal species richness
284   (*S*), representing potential leopard prey species, was estimated for each surveyed community
285   using a non-parametric incidence-based estimator Jackknife with order one (Bunge &
286   Fitzpatrick, 1993). Livestock and other domestic species were excluded from analyses. We

287 calculated Simpson's (*Ds*) and Shannon-Wiener (*H'*) diversity indices for each community using
288 global RAI values in the package 'vegan' in R statistical software (see Table S2; Oksanen et al.,
289 2019). Simpson's diversity index is most sensitive to changes in more common highly abundant
290 species, while the Shannon-Wiener diversity index is most sensitive to changes in rare less
291 abundant species (Magurran, 2004). Community structure plots representing the RAI as a factor
292 of trophic level and mean adult body weight of potential prey species were also constructed.
293 Jaccard's Index (*J*) and the Sørensen's Coefficient (*CC*) were calculated as measures of
294 similarity, directly comparing Piketberg and the Cederberg, using the following formulae:

295
$$J = \frac{A}{[A + B + C]} \qquad\qquad CC = \frac{2A}{[2A + B + C]}$$

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

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

302 *Occupancy modelling*

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

305
$$\psi_{na\ddot{\imath}ve} = \frac{\#\ of\ sites\ detected}{\#\ of\ sites\ sampled}$$

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

316 All continuous covariate values were scaled into standardized z-scores (Bruggeman et al., 2016).
317 Multi-collinearity was tested for by calculating variance inflation factors (VIF), whereby
318 covariates with VIF scores greater than three were removed (Wang et al., 2018). A global

319 occupancy model that included all ecologically relevant covariates (see Table S1) was applied to
320 the subsets of data for each species and tested for goodness-of-fit (MacKenzie & Bailey, 2004).
321 Subset data for each species that had the closest over dispersion statistic (ĉ) to 1 (extreme values
322 over (> 3) or under 1 (< 0.90) indicate poor fit of the data) and an insignificant chi-square
323 probability (χ^2p > 0.05) was chosen for further occupancy analyses (see Table S3; Mazerolle,
324 2017). This showed maximum model fit without over compressing statistical power of the data
325 (Burnham & Anderson, 2004; MacKenzie & Bailey, 2004). Our study violates the assumption of
326 spatial autocorrelation and independence of camera-trap sites, which means that our results will
327 be interpreted within the context of area used (i.e. space-use) rather than area occupied
328 (MacKenzie & Nichols, 2004).

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

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

Results

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

356   abundance values were employed, providing equal weight to both communities, therefore
357   allowing comparison.

Species richness

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

366   [Insert Figure 2 here]

Community structure

368   Differences in community structure were largely complementary, providing a similar pattern
369   across trophic guilds for both the Cederberg and Piketberg (Figure 3). The same number of
370   carnivore species were detected in both regions (n = 10), but no Cape fox (*Vulpes chama*, Smith,
371   1833) or large grey mongoose (*Herpestes ichneumon*, Linnaeus, 1758) were recorded in the
372   Cederberg, whereas black-backed jackal and water mongoose (*Atilax paludinosus*, Cuvier, 1826)
373   were not detected in Piketberg. Herbivores were the most frequently encountered guild across
374   both regions; more herbivorous species were encountered in the Cederberg (n = 13) than in
375   Piketberg (n = 11). Main leopard prey species (i.e. baboon, duiker, grysbok, hyrax, klipspringer,
376   porcupine, and rhebok) were all accounted for in both communities (Table S2).

377   Across all guilds, global trap rates (RAIs) for species detected were generally higher in Piketberg
378   (Figure 3 & Table S2). Noteworthy exceptions included hyrax (Cederberg: 4.05; Piketberg:
379   3.16), klipspringer (Cederberg: 3.56; Piketberg: 2.41), and rhebok (Cederberg: 0.84; Piketberg:
380   0.14). A marked difference was the higher RAIs of all carnivores > 4 kg – including leopard
381   (Cederberg: 3.52; Piketberg: 4.65) – as well as most medium (> 0.5 kg and < 100 kg) herbivores,
382   in the Piketberg region (Figure 3 & Table S2). Baboons were the most frequently detected
383   species across both communities (Cederberg: 608 events; Piketberg: 592 events), followed by
384   hyrax in the Cederberg (410 events) and porcupine in Piketberg (540 events). No single species
385   dominated (i.e. > 50% of total trap rates) in any of the two communities.

386   [Insert Figure 3 here]

387   High levels of similarity between the two study regions were shown by both the Jaccard's Index
388   ($J = 0.73$) and Sørensen's Coefficient ($CC = 0.85$). The Jaccard's Index suggested that 73%
389   similarity exists between the contrasting communities. Similarly, the Sørensen Coefficient

390 suggested that the ecological distance that separate the two regions is merely 15%, supporting
391 close relatedness of ecological make-up in each community.

392 *Spatial behaviour*

393 Camera-trap stations were excluded from occupancy (i.e. space-use) analyses when cameras
394 were operational for < 80% of occasions (see Figure 1). Baboon and rhebok were excluded due
395 to insufficient model fit (Table S3). Only strong relationships with space-use and detection
396 probabilities are discussed (see Table 1). In essence, factors that strongly influenced the spatial
397 dynamics of leopards and their main prey species in the Cederberg were primarily environmental
398 (56%), whereas anthropogenic (32%) and biotic variables (12%) played a less significant role
399 (Table 1). In contrast, anthropogenic variables (41%) dominated in Piketberg relative to notable
400 influences by biotic (36%) and environmental (23%) factors (Table 1).

401   [Insert Table 1 here]

402   *Leopard*
403 Leopards occurred across the landscape in both communities and were detected at 55 camera-
404 trap stations in Piketberg and 60 stations in the Cederberg, providing naïve occupancy estimates
405 of 0.852 (Piketberg) and 0.833 (Cederberg) respectively. The spatial dynamics of leopards
406 differed between the Cederberg and Piketberg, except for both leopard populations preferring to
407 utilise areas further away from human habitations (Table 1; Figures 4A & 5A). In the Cederberg,
408 leopards also preferred areas in closer proximity to permanent rather than seasonal water sources
409 (Table 1; Figure 4B) but were more likely to be detected further away from water (Table 1;
410 Figure 4E). Furthermore, leopards of the Cederberg were generally less likely to be detected in
411 areas where sympatric meso-carnivores were more abundant (Table 1; Figure 4C) and at higher
412 altitudes (Table 1; Figure 4D). In Piketberg, leopards were less likely to be detected if present at
413 sites characterised by Sandveld vegetation and in areas utilised by livestock (Table 1; Figures
414 5B, 5C, 5D & 5E).

415   [Insert Figure 4 here]

416   [Insert Figure 5 here]

417   *Main prey species*
418 The space-use of grysbok, hyrax, klipspringer, and porcupine were influenced by slightly
419 different factors in the primarily protected Cederberg and agriculturally transformed Piketberg
420 (Table 1). None of the variables we considered were found to strongly influence duiker space-
421 use (Table 1). In the Cederberg, grysbok preferred areas farther away from roads, porcupine
422 preferred areas of older vegetation, while hyrax preferred areas characterised by Karoo
423 vegetation and seemingly avoided areas where caracal and black-backed jackal were abundant.
424 In Piketberg, both hyrax and klipspringer avoided areas where caracal were more prevalent

425 (black-backed jackal are absent), but porcupine appeared to prefer areas that had greater caracal
426 presence.

427 The detection probabilities (i.e. detectability) of these prey species were affected by various
428 combinations of factors across the greater landscape (Table 1). In both study regions, duiker
429 were more likely to be detected (if present) nearer to human habitations and at lower altitudes,
430 grysbok were more likely to be detected in closer proximity to roads, and klipspringer were more
431 likely to be detected where meso-carnivores were less abundant. Considering only the
432 Cederberg, detectability of duiker was greater farther away from water sources and lower in
433 areas consisting of older vegetation. Detection of grysbok was more likely in areas that showed
434 signs of anthropogenic disturbance, but less likely at sites characterised by Karoo vegetation.
435 Similarly, the probability of detecting porcupine was also lower in areas of Karoo as well as
436 older vegetation, and greater in areas closer to roads. By contrast, the detectability of both hyrax
437 and klipspringer in the Cederberg was greater within the Karoo biome. Furthermore, hyrax were
438 more likely to be detected at lower altitudes and farther away from roads, whereas the probability
439 of detecting klipspringer was less at anthropogenically disturbed sites. In Piketberg, detection
440 probability of klipspringer was greater closer to water, particularly permanent water sources.
441 Both klipspringer and duiker were also more likely to be detected in the vicinity of roads in this
442 region. Additionally, duiker, as well as hyrax, were less likely to be detected where leopard RAI
443 was greater. Instead, hyrax detectability increased as caracal RAI increased. On the other hand,
444 grysbok in Piketberg were more likely to be detected in areas where leopards were seemingly
445 more abundant. Their detection probability was also greater at higher altitudes and in areas closer
446 to human habitations. Detectability of porcupine, however, was lower nearby human habitations.
447 Yet, porcupine were more likely to be detected in areas that showed other signs of anthropogenic
448 disturbance across the agriculturally transformed region.

Discussion

Prevalence of leopards

451 Contrary to expectations, our results, in terms of both relative abundance indices (RAI:
452 Cederberg: 3.52; Piketberg: 4.65) and naïve occupancy ($\psi_{naïve}$: Cederberg: 0.833; Piketberg:
453 0.852), suggest that leopards are at least as relatively widespread across the agriculturally
454 transformed Piketberg landscape, and potentially even more abundant, than they are in the
455 primarily protected Cederberg region. We similarly observed greater relative abundances of all
456 carnivorous species > 4 kg shared between the two communities (Figure 3 & Table S2).
457 Assuming comparable average activity levels, leopards of Piketberg may therefore occupy
458 smaller or more overlapping home ranges than leopards found in the Cederberg (refer to Müller
459 et al., 2022b). Recently, Snider et al. (2021) showed that it is indeed common for free-roaming
460 leopard home-range size to be smaller (inferring greater density) within areas of greater human
461 population density. Alternatively, should activity levels greatly differ between the two

462 subpopulations, leopards could also occupy larger home ranges in Piketberg (Neilson et al.,
463 2018; Rogan et al., 2019). Since the relationship between occupancy (or space-use), abundance,
464 and density is influenced by the number of individuals, home range size, and the degree of
465 spatial overlap between individuals, neither relative abundance nor the space-use parameter can
466 be used to ascertain differences in density with absolute certainty (Rogan et al., 2019).
467 Nonetheless, greater predator abundances can only be sustained by a greater relative carrying
468 capacity (i.e. prey availability). Higher RAIs were also noted in Piketberg compared to the
469 Cederberg for most medium sized (> 0.5 kg and < 100 kg) herbivores (Table S2), which are
470 regarded as the primary prey component for leopards (Hayward et al., 2006). Therefore, prey
471 populations in Piketberg appeared sufficient to facilitate and sustain relatively greater, potentially
472 denser, and at least as equally successful predator populations to those found in the Cederberg.
473 Notable differences that we observed in the RAIs of main leopard prey species between the two
474 study regions, however, suggests that leopard diet composition is likely to differ (based on
475 availability; Hayward et al., 2006) in the agriculturally transformed landscape.

476 The main prey species considered in this study are known to comprise approximately 85% of the
477 biomass consumed by leopards in the Cederberg (Müller et al., 2022a), while in other areas of
478 the Western Cape they comprise as much as 91% (Boland) and as little as 57% (Little Karoo) of
479 leopard diets (Mann et al., 2019). Grey rhebok, klipspringer, and rock hyrax were more abundant
480 in the Cederberg, while Cape grysbok, Cape porcupine, chacma baboon, and common duiker
481 were more abundant in Piketberg (Table S2). Leopards in the Cederberg appear heavily reliant
482 on hyrax and klipspringer in particular, which together constitutes ~61% of biomass consumed
483 (Martins et al., 2010; Müller et al., 2022a). Despite lower relative abundances recorded for both
484 these prey species in Piketberg (Table S2), where leopard diet composition remains unknown,
485 the leopard population here appeared unaffected. Our findings thus suggest the persistence of
486 leopards in this agriculturally transformed region, highlighting the adaptability, but also the
487 potential vulnerability, of these large apex predators. Leopards in the Soutpansberg and
488 Waterberg mountains (Limpopo Province) of South Africa have also been shown to thrive
489 outside of protected regions (Chase Grey, Kent & Hill, 2013; Swanepoel, Somers & Dalerum,
490 2015), as is the case across a densely populated agricultural landscape in India (Athreya et al.,
491 2013). Therefore, together with our results, it is evident that a landscape level approach is needed
492 to ensure that the appropriate conservation policies, laws, and practices are implemented
493 (Athreya et al., 2013) to ensure the safeguard of leopards throughout the entirety of their
494 distributional range and not just in protected areas. The importance of protected regions is,
495 however, not to be undermined (see Mohammadi et al., 2021).

496 **Natural prey species availability**

497 Our camera surveys appear to have recorded almost all natural potential prey species (mammals
498 > 0.5 kg) present, as the number of species captured was very close or equal to the total number
499 estimated in both communities. Community composition of potential prey species did differ, but

500   niche composition remained relatively intact across both regions, and each supports complete
501   communities of carnivores and herbivores (Figure 3). Generally, carnivores do not play a
502   significant role in leopard diet in the Western Cape (Martins et al., 2010; Drouilly, Nattrass &
503   O'Riain, 2018; Mann et al., 2019; Müller et al., 2022a), although elsewhere small carnivores are
504   commonly killed (Palomares & Caro, 1999; Hayward et al., 2006). Herbivores unique to each
505   community in our study (gemsbok in Cederberg; kudu in Piketberg: Table S2) were both large
506   antelope species (> 100 kg) which also generally do not constitute a major component of leopard
507   diet in the Western Cape, except in the Little Karoo (Martins et al., 2010; Drouilly, Nattrass &
508   O'Riain, 2018; Mann et al., 2019; Müller et al., 2022a). Here, their marked presence in leopard
509   diet has been attributed to land-use change, characterised by an increase in game farming in
510   recent years (Mann et al., 2019). It is however improbable that the very low abundances (Table
511   S2) and limited distributions (detected at only one station each) we recorded for these large
512   antelopes in Piketberg would effectively support its leopard population. Instead, predation on
513   these introduced individuals would be likely to ultimately result in farmer-predator conflict and
514   increase the level of risk that leopards are exposed to (Constant, Bell & Hill, 2015). Hence, the
515   minor differences observed in potential prey species composition and richness between the
516   Cederberg and Piketberg are unlikely to substantially influence leopard diet, and consequently
517   population persistence, in the latter.

518   **Variance of main prey species**

519   Leopards in Piketberg are more likely to rely on alternative main prey species to those primarily
520   utilised in the Cederberg, based on observed differences in their perceived availability in each
521   community (Table S2). By considering the factors that strongly affects habitat use of main prey
522   species (Table 1), we broadly infer some potential underlying drivers of these differences. Due to
523   the inability to model probabilities of space-use and detection for baboon and rhebok, we did not
524   speculate on probable causes for differences in their availability (i.e. RAIs). It should also be
525   noted that our results for hyrax may be unintentionally skewed because of their restricted habitat
526   (being confined to rocky outcrops; Skinner & Chimimba, 2005) not being accounted for in our
527   camera set-up procedures; we advise caution in interpretation thereof.

528   Unsurprisingly, the relative impact on prey species by anthropogenic factors accompanying
529   agricultural practices (e.g. roads, disturbances, habitations) was greater in Piketberg, but not all
530   species were negatively influenced (Table 1). In essence, anthropogenic drivers were generally
531   more likely to strongly influence preferred main prey species of the Cederberg (hyrax and
532   klipspringer) in a negative manner, but alternative main prey species (duiker, grysbok, and
533   porcupine) appeared less sensitive, some even showing a potential preference for disturbed sites.
534   These alternative prey species are therefore likely to play a relatively larger role in leopard diet
535   and facilitation of the leopard population in Piketberg. The greater perceived abundance of
536   duiker, grysbok, and porcupine in the agriculturally transformed region may further be facilitated
537   by a preference for readily available crop food resources as these species are known to frequent

538   the fringes of agricultural land (Birss, Relton & Selier, 2016; Bragg & Child, 2016; Palmer et al.,
539   2016). Elsewhere in the Western Cape, however, it has recently been shown that duiker and
540   grysbok both remain dependent on natural vegetation even within severely transformed
541   landscapes (Jansen van Vuuren, Fritz & Venter, 2022). We therefore believe that suitable natural
542   habitat within the mosaic Piketberg landscape plays a pivotal role for sustaining these species.
543   Thus, we promote the maintenance of natural vegetative corridors within and between
544   transformed lands. Remaining natural vegetation in Piketberg can generally be considered denser
545   than across the Cederberg, thereby having the potential to further cater for grysbok and
546   porcupine which are both known, and shown by this study, to require sufficient vegetative cover
547   (Bragg & Child, 2016; Palmer et al., 2016). In contrast, the sparser Karoo vegetation of the
548   Cederberg appear to be favoured by hyrax and klipspringer (Birss et al., 2016; Visser &
549   Wimberger, 2016). These two species also appeared to be the most affected by top-down
550   influences of predators as both species in both communities seemingly avoided areas heavily
551   utilised by caracal and black-backed jackal, resulting in an indirect spatial overlap with leopards
552   in the Cederberg. Interestingly, leopard RAI strongly influenced main prey species in Piketberg
553   only, exhibiting direct overlap with grysbok. Yet again, hyrax and duiker in Piketberg appeared
554   to be influenced in an opposing manner. In the Cederberg and elsewhere, hyrax are particularly
555   favoured as prey by both leopard and caracal (Hayward et al., 2006; Müller et al., 2022a). It is
556   thus also plausible that hyrax may in fact experience significant predation pressure and therefore
557   their numbers and activity may appear relatively limited in areas shared more frequently with
558   leopards in Piketberg (Wittmer, Sinclair & Mclellan, 2005).

559   **Livestock – An alternative food source?**

560   Aside from alternative main prey species playing an important role, unnatural prey (i.e. livestock
561   or domestic species) might also supplement leopard diet in Piketberg. In a national park in
562   Pakistan and a human-dominated landscape in India for example, leopards have previously been
563   shown to be almost completely dependent on livestock and other domestic species as prey
564   (Shehzad et al., 2015; Athreya et al., 2016). Our decision to exclude livestock and other domestic
565   species from abundance analyses was because the vastly greater use of livestock proof fences in
566   the Piketberg region prevented accurate and comparable detection of livestock at camera-trap
567   stations. While fences do not prevent the movement of leopards across a landscape, the energetic
568   costs to leopards that accompany their presence may be a driving factor for the killing of more
569   livestock (Wilmers et al., 2017). Müller et al. (2022a) showed that 7% biomass of leopard diet in
570   the Cederberg was comprised of livestock. Subsequently, we believe a greater proportion can be
571   expected in Piketberg, which is a conclusion that seems to be supported by higher levels of
572   livestock predation events reported in recent years (C Luyt - Community Outreach Officer at the
573   Cape Leopard Trust, 2020, pers. comm.). Although not found to be strongly correlated in either
574   region, the inverse relationship between space-use by leopards and presence of livestock in the
575   two contrasting study regions (Table 1), is noteworthy. Leopards in the Cederberg tended to
576   avoid areas with signs of livestock, while in Piketberg they appear to have shown a greater

577   preference for areas with livestock. This observation could suggest a plausible tendency for
578   greater reliance on livestock by leopards in Piketberg. In the Cederberg, livestock roam more
579   freely but tend to be guarded by herders, whereas in Piketberg they are generally fenced and
580   unguarded. Unguarded, fenced livestock that are not completely predator-proofed may result in
581   leopards being attracted to livestock as prey, especially when preferred natural prey abundances
582   are low (Odden, Nilsen & Linnell, 2013; Khorozyan et al., 2015). This may subsequently result
583   in an increase in illegal retaliatory killings, making the leopard population in Piketberg
584   particularly vulnerable (Inskip & Zimmerman, 2009; Soofi et al., 2022).

585   Importantly, if livestock serve as regular prey, this has the potential to result in less pressure and
586   reduced ecological regulation of natural prey species, regarded as agricultural pests (Norton,
587   1980; Kingdon, 1982; Estes, 1991; Skinner & Chimimba, 2005). Examples of this has been
588   described with other apex predators like snow leopards (*Panthera uncia*, Schreber, 1775) in
589   Nepal and dingoes (*Canis lupis dingo,* Meyer, 1793) in Australia (Johnson & Wallach, 2016;
590   Shrestha, Aihartza & Kindlmann, 2021). Conversely, leopards that are less reliant on livestock as
591   prey, provided sufficient preventative measures for livestock predation are employed, can
592   partially limit population explosions of their natural prey species (O'Bryan et al., 2018).
593   Effective preventative mitigation of conflict with crop pests (i.e. prey species) may also cater for
594   leopards, offering sufficient natural prey availability in the future which may minimise livestock
595   losses (Odden, Nilsen & Linnell, 2013; Khorozyan et al., 2015). Hence, leopards and their prey
596   species can be regarded as assets on a landscape scale, and pro-active (preventative and non-
597   lethal) measures employed together by livestock and crop farmers in an agricultural community
598   can thus benefit them both instead of either one indirectly inducing conflict onto the other. We
599   therefore agree with Du Toit, Cross & Valeix (2017) that a shift in attitude towards asset
600   management, rather than problem control by means of retaliatory killings, will be advantageous
601   as the removal of conflict-prone species is likely to be counter-productive for the community
602   (Conradie & Piesse, 2013; Lennox et al., 2018).

Impacts on leopard behaviour

604   Besides potential for retaliatory killings of leopards, a further direct negative impact due to
605   humans was reflected by the avoidance of human habitations by leopards in both study regions
606   (Table 1; Figures 4A & 5A). This reiterates that anthropogenic development is responsible for
607   habitat loss (Swanepoel et al., 2013; Jacobson et al., 2016). Environmental factors that directly
608   dictated the spatial dynamics of leopards differed between the two regions (Table 1). Greater
609   detectability further away from water in the Cederberg, where sources are presumably more
610   limited, can be explained since leopards are largely independent of water (Bothma, 2005).
611   Leopards in this region did however show a preference for areas closer to permanent (e.g. rivers;
612   Table S1) rather than seasonal (e.g. streams; Table S1) water sources, but this is likely to be a
613   simple consequence of the seasonal water sources being dry and unusable at the time of our
614   study. The lower detection probability of leopards in Sandveld vegetation and areas presumably

615   used for grazing in Piketberg indicate that fine-scale habitat utilisation by leopards is likely to be
616   selective and affected by agricultural activities. The influence of altitude observed in the
617   Cederberg is assumed to be a consequence of the slightly higher density recorded for leopards in
618   the region during the summer months, which relates to individuals occupying smaller home
619   ranges on the more accessible lower mountain slopes at this time of year (Müller et al., 2022b).
620   Finally, the relationship we observed between leopards and meso-carnivores in the Cederberg is
621   consistent with the conclusions of Müller et al. (2022a): caracal (meso-predator) tend to avoid
622   leopards (apex predator) in time and space. Interestingly, the availability of natural main prey
623   species did not directly dictate spatial utilisation by leopards, which is probably because leopards
624   (and natural prey) occurred widely across the study area. It is important to note that the impacts
625   we observed on the behaviour of various main prey species, both environmental and
626   anthropogenic, do have the potential to indirectly affect leopards going forward. Therefore,
627   continuous monitoring and evaluation of the environmental and anthropogenic factors affecting
628   the ecology of both leopards and their natural prey is of vital importance to ensure the
629   persistence of leopards in both protected and unprotected areas.

630   **Study limitations**

631   Potential criticisms of our study are that data were collected roughly two years apart, and that we
632   investigated factors influencing behaviour only at a single spatial scale. We are aware that
633   community structure could be influenced by weather on a seasonal or annual basis. The Western
634   Cape experienced a relatively dry year (South African Weather Service, 2021) prior to the
635   Cederberg survey and recorded precipitation of 212.9 mm below the annual mean (2017; Data
636   provided by www.meteoblue.com) in the region. A precipitation anomaly of 139.9 mm below
637   the mean (2019; Data provided by www.meteoblue.com) was also noted prior to the survey in
638   the Piketberg region. Nonetheless, Müller et al. (2022b) showed that the leopard population in
639   the Cederberg remained relatively stable during the decade prior to, and including, our study
640   period. Currently, the same quantitative insight does not exist for the Piketberg community,
641   highlighting a need for long-term population monitoring. Ideally, ecological modelling should
642   aim to incorporate different orders of scale (e.g. Pitman et al., 2017), but this is not always
643   practical. We concur that spatial scale must, however, be accounted for in conservation decision-
644   making.

645   # Conclusions

646   Our findings exemplify how severely transformed, commercial agricultural regions have the
647   potential to facilitate biological diversity – including apex predators – to (at least) the same
648   standard as analogous protected landscapes (also see Linell, Swenson & Anderson, 2001).
649   Indeed, no real differences were apparent between the potential prey species composition or
650   richness, or the prevalence of leopards, in the agriculturally transformed Piketberg and the
651   primarily protected Cederberg communities. Despite the preferred prey species of leopards in the

652 Cederberg being relatively less abundant in Piketberg, the leopard population here seemingly
653 persevere. We believe that greater utilisation of alternative main prey species to those preferred
654 in the Cederberg, likely further subsidised by livestock, facilitates persistence of the Piketberg
655 leopard population. Consequently, this adaptation is a probable driving factor of high levels of
656 human-wildlife conflict. Therefore, in the context of mixed-farming communities, we argue that
657 a holistic multi land-use, multi-species (predator and prey), pro-active management approach,
658 that encourages co-existence and aims to limit the cascade of ecosystem effects that could follow
659 human-induced changes to the landscape, can benefit both livestock and crop farmers.
660 Ultimately, such a collaborative and holistic approach can provide incentive to conserve apex
661 predators and their prey and is therefore useful to ensure the conservation of apex predators on
662 working lands worldwide. Furthermore, we also provide insights on the different combinations
663 of factors influencing the spatial dynamics of leopards and their main prey species. In essence,
664 this study can be used to inform conservation policies that aim to cater for free-roaming leopards
665 in commercial agricultural landscapes, and act as a baseline for ecological monitoring of the
666 Piketberg community, thereby guiding adaptive management going forward. We encourage
667 further detailed investigation of the leopard population in Piketberg, including density, home-
668 range, population structure, dietary and human-wildlife (both leopards and their prey) conflict
669 analyses, to further inform local conservation management decision-making and maintain its
670 leopard population into the future.

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1091 **Figure legends**

1092 **Figure 1:** Maps showing the location of the Western Cape province within South Africa (a), and
1093 the proximity of the survey areas within the Western Cape (b). Main map shows the location of
1094 camera-trap stations for both Cederberg and Piketberg. Failed camera-trap stations (because of
1095 major camera malfunctioning, fire, other damage, or theft) are noted. Formally proclaimed
1096 protected areas (CapeNature reserves) are also highlighted.

1097 **Figure 2:** Rarefied species accumulation curves for medium-to-large (> 0.5 kg) terrestrial
1098 mammals (i.e. potential leopard prey species) photographed in the primarily protected Cederberg
1099 and agriculturally transformed Piketberg regions. Both curves approach an asymptote, indicating
1100 sufficient sampling effort.

1101 **Figure 3:** Distribution of medium-to-large (> 0.5 kg) terrestrial mammals (i.e. potential leopard
1102 prey species) in the Cederberg and Piketberg on the basis of body size and trophic category.
1103 Each circle represents a species in functional space. The size of the circle is proportional to the
1104 trapping rate (RAI) for that species.

1105 **Table 1:** QAICc weights (*w*) for covariates from well-supported models (*w* > 0.10 and QAICc <
1106 2) for each species (leopard + main prey) in each community. Either the direction of the
1107 relationship for covariates from the best fit models or the parameter probability estimate (±
1108 standard deviation) for top models are indicated in parentheses.

1109 **Figure 4:** Detection and space-use (i.e. occupancy) probabilities for leopards with regards to
1110 variables with strong associations in the Cederberg.

1111 **Figure 5:** Detection and space-use (i.e. occupancy) probabilities for leopards with regards to
1112 variables with strong associations in Piketberg.

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.

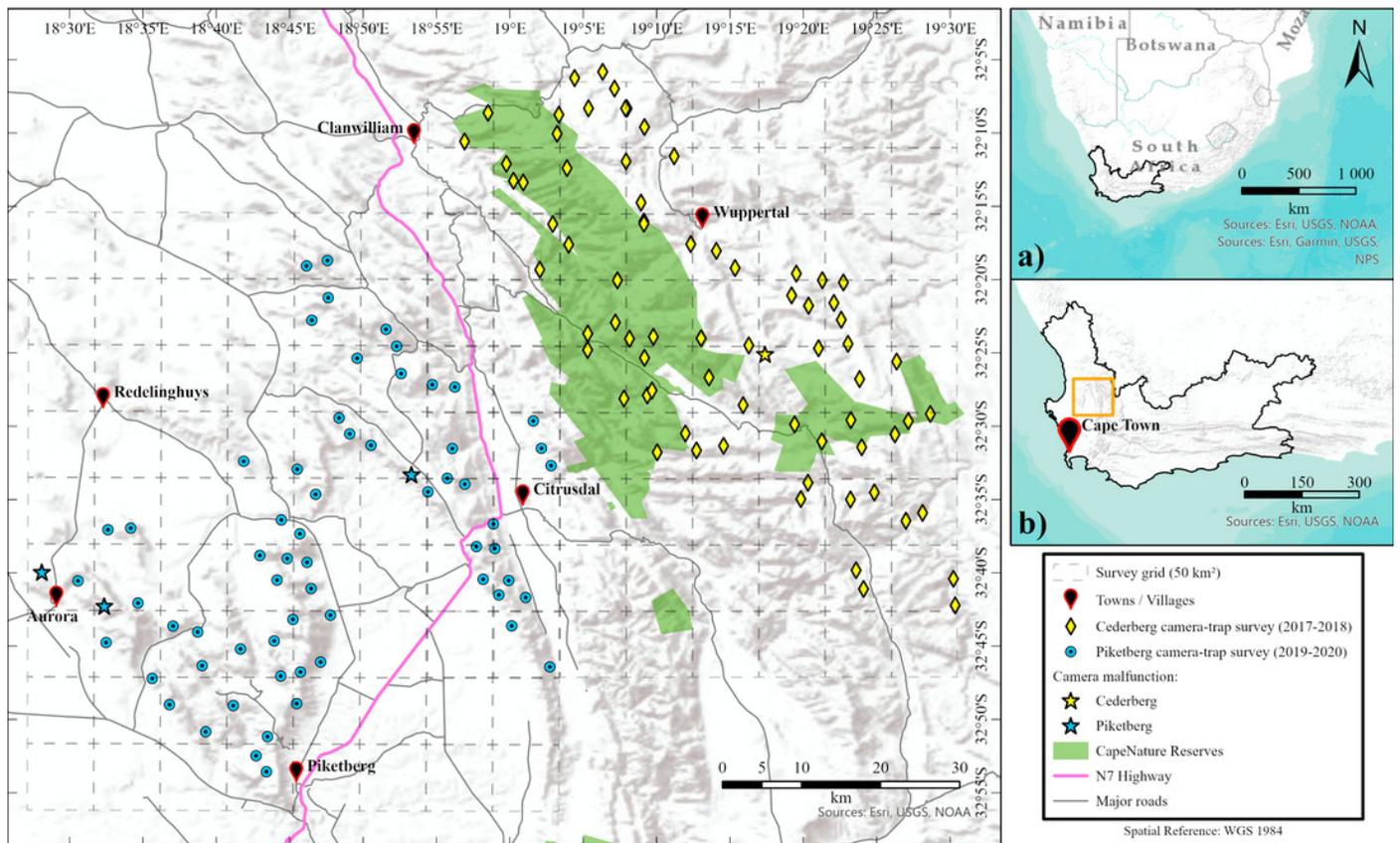



Figure 2

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.

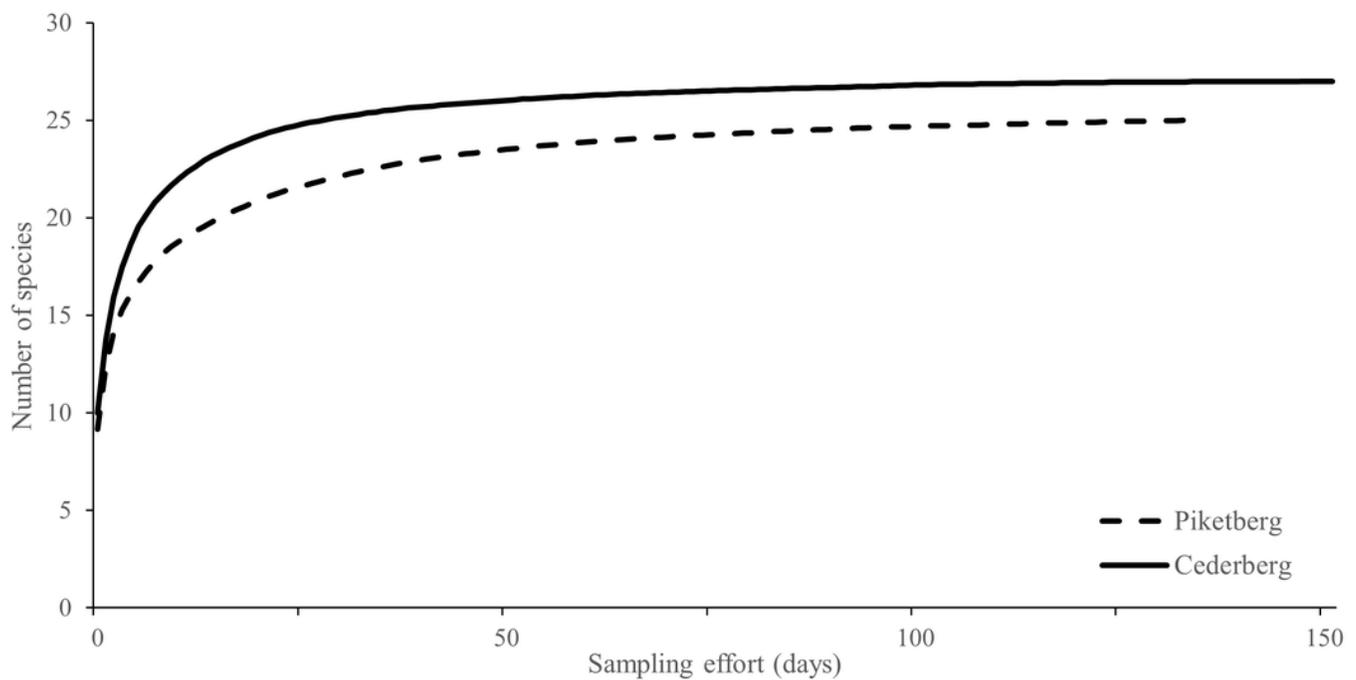



Figure 3

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.

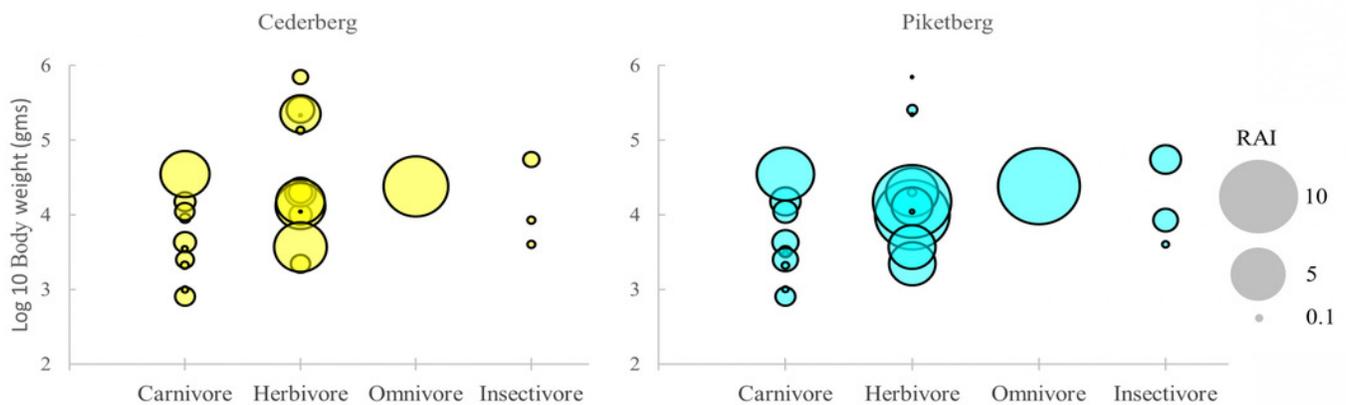



Figure 4

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

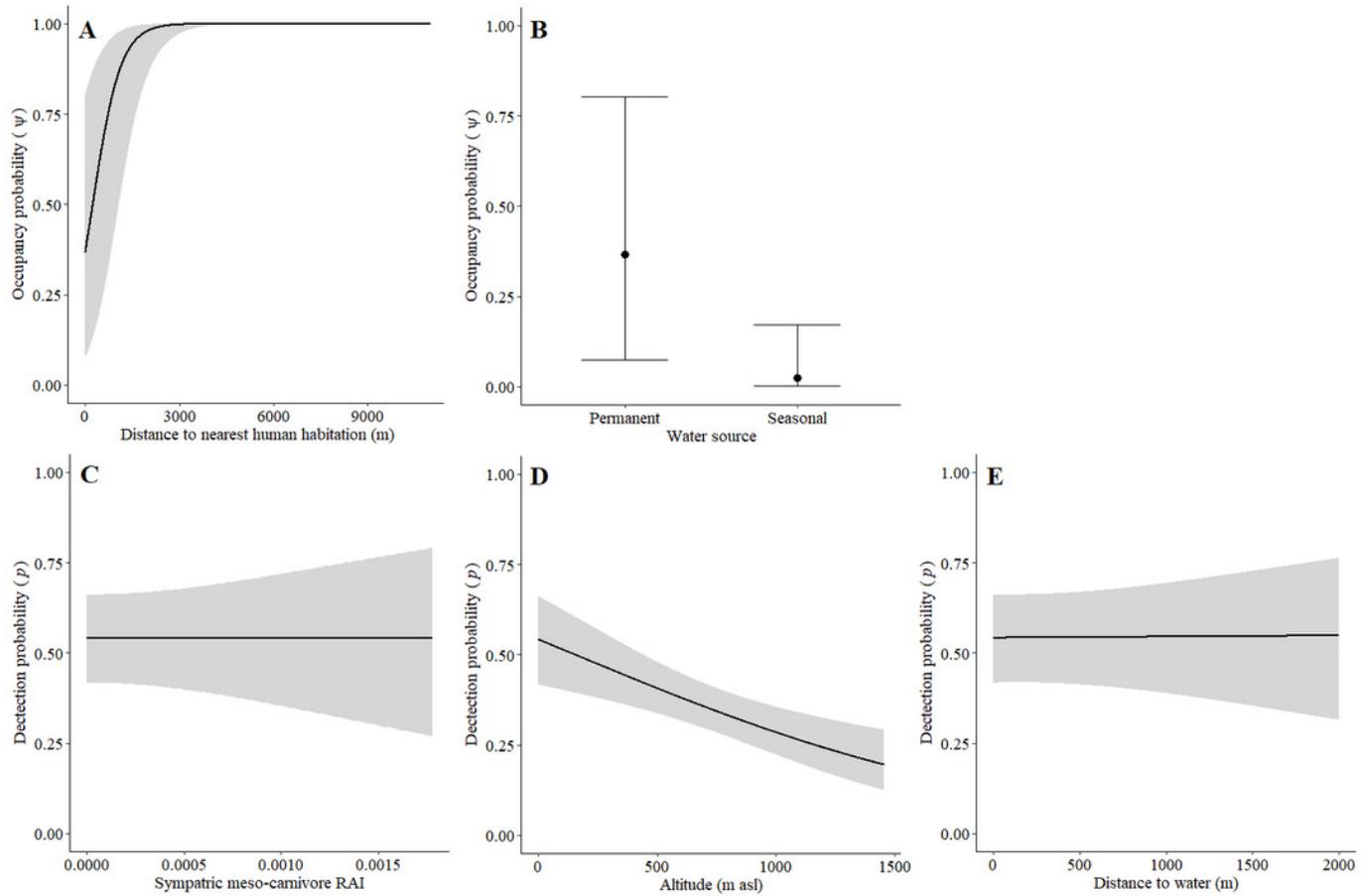
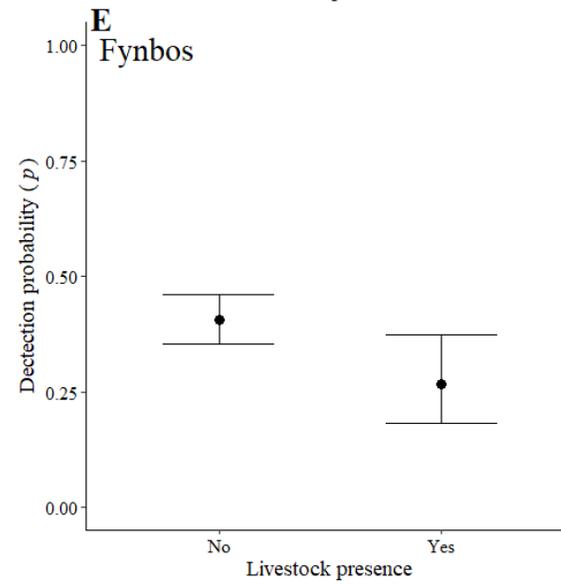
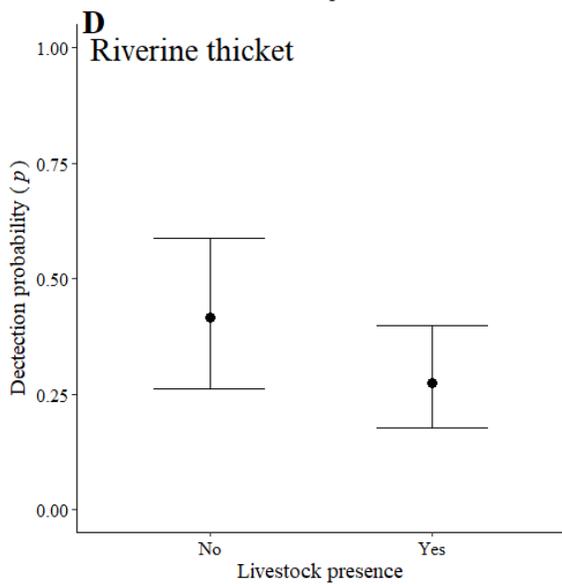
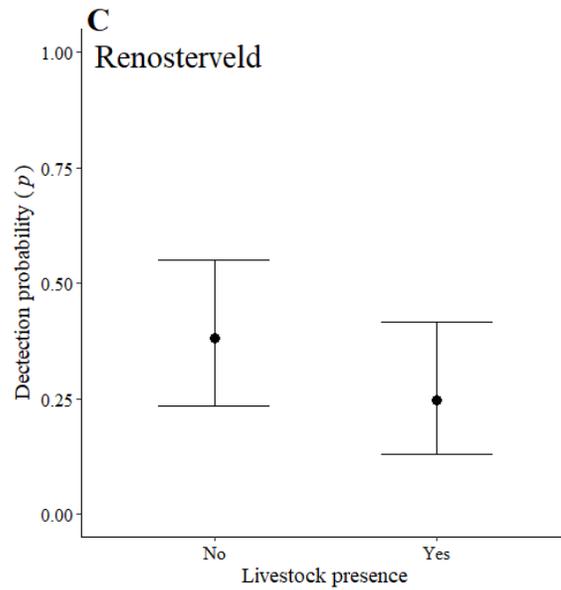
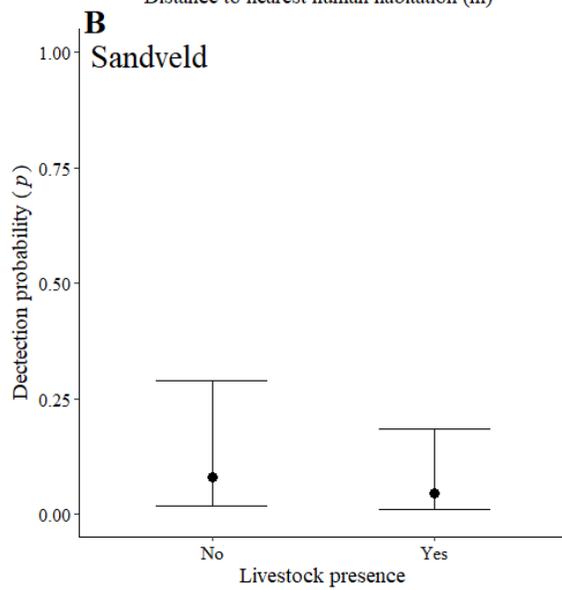
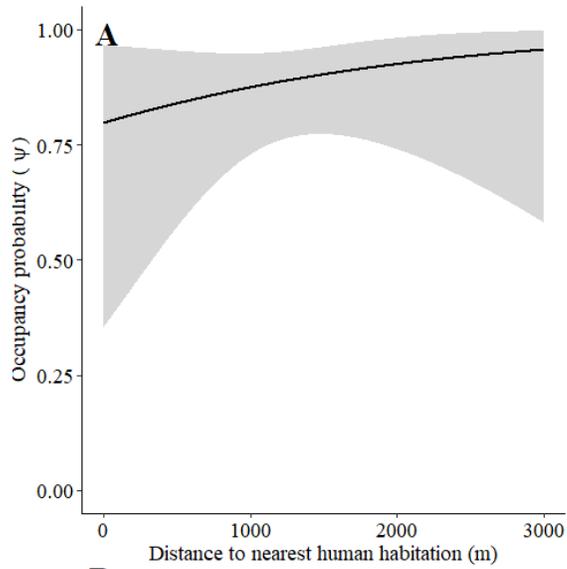



Figure 5

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

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 (+)*	

Species	Param	Covariate	Col1	Col2
		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	

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

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

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