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Review

The Recolonisation of the Piketberg Leopard Population: A Model for Human–Wildlife Coexistence in a Changing Landscape

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Abstract: Important metapopulation dynamics are disrupted by factors such as habitat loss, climate change, and human-induced mortality, culminating in isolated wildlife populations and threatening species survival. Source populations, where birth rates exceed mortality and connectivity facilitates dispersal, contrast with sink populations, where mortality outstrips births, risking localised extinction. Recolonisation by individuals from source populations is pivotal for species survival. The leopard is the last free-roaming apex predator in South Africa and plays an important ecological role. In the Eastern and Western Cape provinces in South Africa, leopard populations have low densities and fragmented population structures. We identified a leopard population that, after being locally extinct for a century, appeared to recolonise an 'island' of mountainous habitat. We aimed to understand potential factors driving this recolonisation using recent camera trapping surveys and historical statutory destruction permits. We employed spatially explicit capture–recapture (SECR) methods to estimate the leopard density and explore potential factors which best explain density. We found that the recently recolonised Piketberg population now exhibits some of the highest densities reported in the region (~1.8 leopards/100 km^2; CI 1.4–2.5). Livestock, human presence, elevation, and the camera trap grid appeared to explain leopard detection rates. When considering the historic data, the re-emergence of leopards in the Piketberg coincided with the cessation of the extensive state-sponsored and state-enabled culling of the species, and the change in land use from livestock production to crop agriculture, which likely contributed to the recolonisation. Elucidating these factors deepens our understanding of leopard metapopulation dynamics in relation to land use and species management and highlights the crucial role of private land and state agencies and associated policies in species persistence.

Keywords: carnivore conservation; density estimates; leopard; metapopulation dynamics; *Panthera pardus*; recolonisation; spatially explicit capture–recapture

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1. Introduction

Having a regulatory role in ecosystems, carnivores serve as ecological engineers and are associated with areas of high mammalian biodiversity [1,2]. Therefore, in places where their populations are low or become locally extinct, this can result in broader ecological disruptions [3]. Habitat loss, prey depletion, genetic isolation, and protracted human-caused mortality have led to declining carnivore populations worldwide [4–7]. Despite being considered the most adaptive of the felids, these threats have resulted in the decline of leopard (*Panthera pardus*) distribution by 75% across its global range and up to 67% of its range in Africa over the last few decades [8], and climate change accelerates this trend [9].

Leopards exist under varying environmental conditions, resulting in localised variations in home range sizes and densities among regions [10–14]. For example, leopard population estimates for the Eastern and Western Cape provinces in South Africa were 467 and 553 adult leopards respectively [11,15]. Within different regions of the two provinces density estimate vary from 0.17 to 1.89 leopards/100 km^2 [10,11,16,17]. However, density estimates alone fail to provide insight into the health and sustainability of metapopulation dynamics across a heterogeneous landscape that encompasses varying levels of anthropogenic impacts and local habitat conditions.

Metapopulation dynamics refers to the interconnected population dynamics of disjunct wildlife populations in heterogeneous landscapes [18,19]. In the Eastern and Western Cape, leopard populations exhibit genetic sub-structuring due to low gene flow, limited habitat connectivity, and human-caused mortality [20,21]. This raises concerns regarding the resilience of leopard populations in the region and illustrates the need for conservation management to promote habitat connectivity and coexistence between humans and carnivores across various land uses [21]. Without facilitating tolerance and coexistence with wildlife by humans, shared habitats could function as sink habitats, thereby increasing the risk of local wildlife population extinctions, reducing the ability for the species to reach nearby populations and habitat patches [22].

Factors driving population density can illuminate the conditions that may result in local population extinctions and the factors which promote the recolonisation of local extinct populations. Leopards were considered locally extinct in the Piketberg, a mountainous area surrounded by highly transformed agricultural landscapes in the Western Cape, South Africa, dating back to the beginning of the 20th century, until novel signs of leopard presence were reported in around the mid-1990s [23]. The region is one of South Africa's oldest livestock and wheat production areas and has a long history of a bounty system and hunting practices aiming at exterminating leopards and other carnivores from the mid-17th to the late 20th century [24]. In the Western Cape, leopard culling was actively encouraged by both a state-funded bounty system that terminated in 1968 and subsidised vermin hunt clubs that were operational until 1994 [24,25].

We aimed to better understand the potential drivers of the recolonisation of this leopard population. We estimated the current leopard density in the Piketberg area of South Africa and assessed potential factors driving these densities. Moreover, to understand historical leopard activity in and around the Piketberg, we reviewed available historical statutory permits issued by the provincial conservation body for leopard culls, as well as reports of livestock damage by leopards between 1975 and 1994. No reliable recorded data regarding leopard activity in the region exist prior to this.

The isolated nature of the current leopard population in the Piketberg leaves them vulnerable to stochastic events such as disease, increasing habitat loss, and high human–wildlife conflicts, which could exacerbate their risk of local extinction [18,26]. We explore the potential determinants of this recolonisation event of leopards based on both the current camera trap survey and historical destruction and hunting permits, considering the role of species and land management in facilitating species persistence and rewilding in transformed landscapes.

2. Materials and Methods

2.1. Study Area

The study took place in the Piketberg, in the Western Cape, South Africa. The Piketberg is a mountainous area surrounded by highly transformed agricultural landscapes locally known as the Swartland, separating it from a nearby natural habitat along the Cape Fold Mountain (CFM) chain to the east (Figure 1). The Piketberg, therefore, due to the transformation of many of the surrounding habitats for crop production, acts as an island of intact habitat for leopards and other wildlife. However, there are narrow strips of habitat at the north-eastern point of the Piketberg that can act as a stepping stone, linking this island to the leopard habitat 'mainland' of the CFM, which hosts known leopard populations [21].

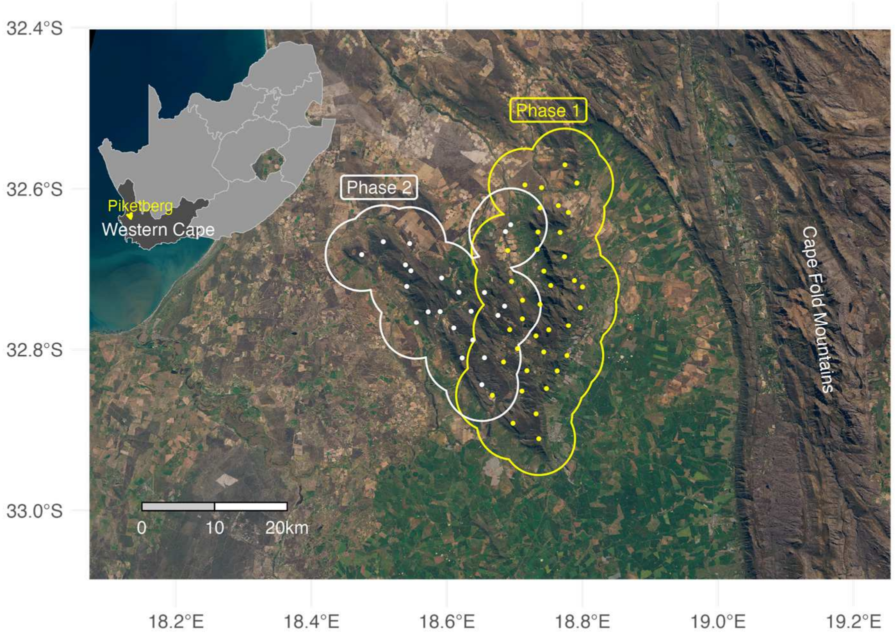

Figure 1. Location of the survey area in the Piketberg and the detector's distribution. Yellow dots represent the location of the camera trap stations in the first survey phase August 2020 to April 2021 (n = 31), and the white dots are the camera station placed during the second survey phase August 2022 to May 2023 (n = 21). The inserts indicate the location of the Western Cape (dark grey shaded area) in South Africa, and the Piketberg is displayed as the yellow area within the Western Cape.

The Piketberg mountain extends approximately 1100 km^2, with the highest peaks reaching 1300 m above sea level, and the valley floors are approximately 70 m above sea level. The higher altitudes are characterised by mountain fynbos vegetation much like the rest of the CFM habitat nearby, while the valley floors host sand plain fynbos and remnant elements of highly threatened west-coast renosterveld present along the eastern slopes [27]. Several villages are dotted across the Piketberg mountain, generally supported by the agricultural sector, which includes crops (e.g., grains, citrus, stone fruits, protea flowers, vineyards) and some livestock production, and by nature-based tourism and recreational land uses (e.g., private nature reserves). There are no formally protected areas within the Piketberg. The area has a winter rainfall regime (May–August) with an average annual precipitation of 501 mm [27].

Leopards are the only free-roaming apex predator present, while mesopredators, such as black-backed jackal (*Canis mesomelas*), caracal (*Caracal caracal*), honey badger (*Mellivora carpensis*), and, more rarely, cape fox (*Vulpes chama*), are present. Leopards were prolific in the Piketberg in 1774 [28]. By the beginning of the 20th century, leopards were locally extinct in the Piketberg mountains and were detected again for the first time in the mid-1990s [23,29].

2.2. Camera Trap Surveys

We used camera traps to detect leopard activity in the study area. Camera traps (Cuddeback, De Pere, WI, USA—Model IR, E or G) were placed approximately 40 cm above the ground at sites considered to have the highest likelihood of capturing leopard activity. Camera traps were placed in a grid pattern set ~2.8 km apart. This resulted in at least one camera trap station installed per female leopard home range (home range size [15]). This ensured there were no gaps large enough to miss a leopard and ensured the maximisation of the capture of leopards at each station. To achieve the assumption of a closed-demographic population, we limited the survey phases to ~90 days [30,31].

To accommodate the large area and number of camera stations required, we conducted two 9-month survey periods. Each 9-month survey was divided into three approximately 90-day phases, totalling three phases of camera trap monitoring within each survey. In the initial survey (survey one), we deployed 72 camera traps across 36 paired stations (Figure 1), including one station equipped with three cameras. These three 90-day phases spanned from August 2020 to April 2021. In the subsequent survey (survey two), conducted from August 2022 to May 2023, we utilised 50 camera traps at 25 paired stations (Figure 1) across the three 90-day survey phases. The difference in the number of cameras used per survey depended on available suitable sites and survey area. All species captured on camera traps were identified by researchers and tagged using digiKam software (version 7.2.0, www.digikam.org, accessed on 25 June 2023), and we extracted the metadata (species, number of individuals, date, time, location) using the '*camtrapR*' package [32] in R environment version 4.3.2 (R Core Team, 2023) with the RStudio interface (Posit team, 2023).

2.3. Density Estimates

2.3.1. Individual Identification

Two independent researchers, experienced in leopard identifications, identified leopards based on their unique fur patterns and distinctive markings (e.g., scars and other notable physical features (Figure 2). All leopard individuals had at least two identical patterns to confirm each individual (Figure 2). We determined each individual's sex based on the presence of testes, dewlap size, and frontal bossing of the skull. When sex could not be distinguished, we noted the sex as unknown [6]. There were no cases where the researchers had different results. Images that could not be confidently identified as a distinct individual were discarded. If the same individual was captured at the same camera trap station within 24 h, it was marked as one occurrence. Only adult leopards were included in the survey due to the high mortality and dispersion probability of juveniles; these could inflate density estimates and bias the demographic representation. Animal ID, trap location, and date were recorded in a matrix for analyses using spatially explicit mark–recapture software ('*secr*' [30]).

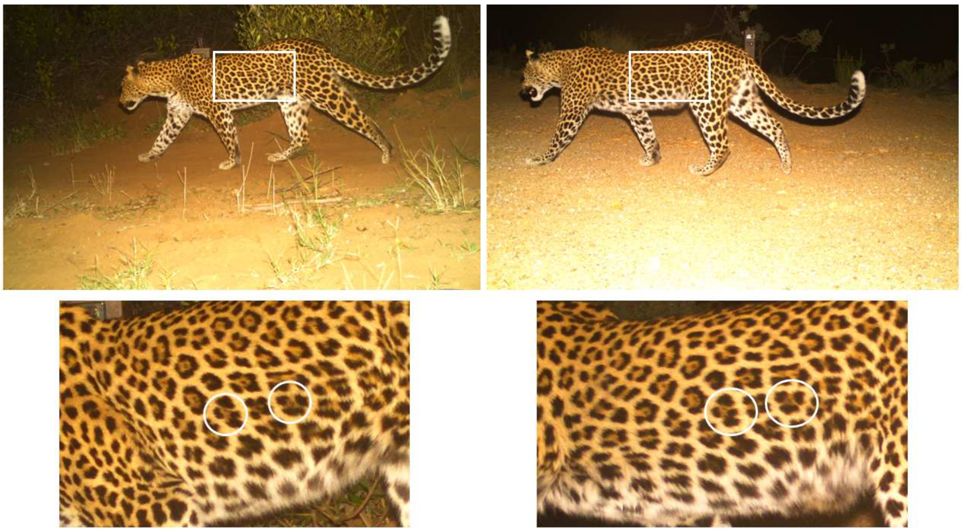

Figure 2. Individual identification of leopards from camera traps using unique fur patterns. The top images illustrate a leopard captured at two trap stations on two occasions. Comparison of the same area of the same flank of the animal (rectangle) is examined, and within that the rosette patterns match (circles), confirming that it is the same individual.

2.3.2. SECR Validation

All analyses were run using R statistical software (version 4.3.2, R Core Team, 2023). We performed the leopard density (D) estimate using spatially explicit capture–recapture (SECR) population density models with maximum likelihood-based inference in the '*secr*' 4.5.0 package [30]. The SECR models estimate D based on capture histories along with spatial locations of captures in a unified manner. We categorised camera traps as 'multi' detectors, allowing the detection of more than one animal per time (24 h) but disallowing repeat occurrences of the same individual.

SECR models estimate two capture probability parameters which jointly determine D. The first is the scale parameter (σ) which controls the 'spread' or 'width' of the detection function; in other words, it captures the rate of the decline in encounter probability as a function of distance from the camera trap. The second is λ_0, which is the basal detection rate, i.e., the rate of detection of an animal whose centre of activity is collocated with the trap. Model fitting was accomplished with the '*secr.fit*' function specified with a negative exponential detection function, the maximisation of full likelihood, and the distribution of camera trap detections specified as a Poisson observation process (Supplementary Materials S1).

For each survey, we used a multi-session model to determine if all model parameters were constant across the phases (i.e., evaluating the effect of phase within survey, T). We then parameterised the models such that the effects of a behavioural learned response ($\lambda_0\sim b$, $\sigma\sim b$); global behavioural learned responses ($\lambda_0\sim bk$, $\sigma\sim bk$); the effect of sex (β_{sex}), as an individual-level covariate ($\lambda_0\sim Sex$, $\sigma\sim Sex$); and landscape- or trap-specific predictor variables (see 'Factors driving density estimates') could be compared to a null model ($\lambda_0\sim 1$, $\sigma\sim 1$) that excluded any of these influences (Supplementary Materials S1). The landscape covariates were included in the model either as continuous habitat masks for modelling density surfaces or trap-specific covariates for developing an understanding of covariate effects on detection parameters. Using QGIS (version 3.12.1), habitat mask layers were sized to the same extent and resolution of 1 km^2 and used to predict a fine-scale resolution density map.

We ranked the best candidate models using Akaike's Information Criterion ($AICc$) corrected for small sample size [33]. We described conclusions about the function of covariates to density responses based on the 95% CI of coefficients and the direction of these. A state-space mask was created to represent the available habitat for leopards with buffer distances calculated with the '*suggest.buffer*' function corresponding to $6 \times \sigma$ [30]. These buffers ensured the inclusion of all home ranges within reach of camera traps and made density estimates more reliable [34,35].

2.4. Factors Driving Density Estimates

We selected several covariates we considered potential drivers of leopard density across the different sites based on the existing literature [11,14,36]: the Relative Abundance Index (RAI) for prey; Euclidian distance to the nearest dwelling (m); nearest river (m); nearest road (m); elevation (m); the RAI for humans; the RAI for livestock; veld type; land-use type; and slope. We calculated an RAI for prey abundance, domestic livestock, and human activity, as the number of independent captures (24 h) taken of each species during the survey period [37]. Potential free-roaming prey for leopards in the mountains of the Western Cape includes ungulates such as klipspringer (*Oreotragus oreotragus*), common duiker (*Sylvicapra grimmia*), grey rhebok (*Pelea capreolus*), Cape grysbok (*Raphicerus melanotis*), and steenbok (*Raphicerus campestris*); rodents such as Cape porcupine (*Hystrix africaeaustralis*); mongoose (*Herpestidae* sp.); and in some instances, baboon (*Papio ursinus*) [38,39]. We included cattle, sheep, and goats when calculating the livestock RAI as leopards are able to prey on calves, as well as small stock. Human presence was included when cameras captured humans, vehicles, or pets.

Large terrestrial carnivores display sex-related differences in their home range sizes and interaction with their environments [36,40]. Differences in the movements of animals based on sex can affect the observation process in density estimation analyses [36]. We factored this into our models by including sex as a covariate in the observation process and accounted for the different capture probabilities for leopards. The duration of each phase was tested within each survey to determine if density estimates varied as a result of the phase period. To determine if the installation of camera traps might influence the behaviour of animals and thereby affect detection rates, we tested if learned responses by animals may correlate to detection.

2.5. Review of Statutory Permits to Assess Historic Leopard Population Status in the Piketberg and Immediate Surrounds

Following the establishment of the Cape Province's Department of Nature Conservation in the 1950s (later known as Cape Nature from 2000 onward), leopards were first excluded from the 'vermin' animal classification in 1968 [25]. From 1975, the Cape Provincial Ordinance 19 of 1974 mandated permits for the destruction or capture of leopards [41], and this was prompted by international efforts to protect the species as it gained protection under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Vermin-hunting clubs continued to receive state subsidies under the Problem Animal Control Ordinance 26 of 1957 until the 1990s, which was only formally repealed from the statutes in 2009 by the Western Cape Provincial Government. To assess historic leopard occurrences in the Piketberg and the surrounding areas, we obtained statutory permits issued in the Western Cape for legal destruction and records of illegal leopard-destruction events during the period from 1975 to 1988 (Supplementary Materials S2). Additionally, we examined regional municipal council problem animal hunter reports of the state-funded vermin hunt clubs from 1989 to 1994, up until their discontinuation in 1994 (Supplementary Materials S2). All data are available online. However, the *xy* coordinates are not provided in the dataset in order to reduce potential risk to species at sites as some species are protected.

3. Results

3.1. Camera Trap Surveys

3.1.1. Survey One

Five stations were excluded in the first survey of the Piketberg, for reasons including theft and malfunctions. The remaining 32 stations were used in the analyses for the first three phases. In total, 11,172 photographs (including false triggers) were obtained, capturing 31 wild mammalian species (Supplementary Materials S3). Once data were filtered by removing false triggers and duplicate images obtained from the paired camera trap station, 5699 images were used, of which, 378 (6.5%) were of leopards (Table 1; Supplementary Materials S3). Phases one, two, and three operated for 92, 91, and 88 consecutive days, capturing 15, 15, and 21 individual leopards on 101, 1033, and 140 occasions, respectively (Supplementary Materials S4). Leopards were captured at 23, 21, and 27 stations during phase one, two, and three, respectively (Supplementary Materials S4).

Table 1. Leopard abundance estimates calculated during each survey phase for the Piketberg region using SECR. SE = standard error; LCI = lower confidence intervals; UCI = upper confidence intervals, *n* = number of individual leopards counted from the camera trap data per phase of each survey.

Site	Survey	Estimate	SE	LCI	UCI	Leopard Images	Used Leopard Images	*n*
Piketberg	Phase 1	30.4	8.3	18.0	51.5	108	107	15
Piketberg	Phase 2	22.7	6.2	13.4	38.4	115	115	15
Piketberg	Phase 3	29.4	7.0	18.6	46.5	156	156	21
Survey 1		27.5	7.2	16.7	45.5	379	378	
Piketberg	Phase 4	25.9	11.8	8.6	41.7	43	38	8
Piketberg	Phase 5	27.4	9.6	14.1	53.3	77	75	12
Piketberg	Phase 6	23.6	9.0	11.4	48.7	42	41	10
Survey 2		25.6	10.1	11.4	47.9	162	154	

3.1.2. Survey Two

Twenty-one stations were used in the final analyses for phases four, five, and six, forming the second survey of the Piketberg. In total, 7040 photographs were obtained, capturing 27 wild mammalian species (Supplementary Materials S3). After processing the photographs and removing duplicates, 2869 images were obtained, of which, 171 (6%) were of leopards (Supplementary Materials S3). In total, eight leopard images were excluded from this survey, as it was not possible to identify individuals from these (Table 1). Phases four, five, and six operated for 92, 92, and 92 consecutive days, respectively, capturing 8, 12, and 10 individual leopards on 23, 42, and 32 occasions (Supplementary Materials S4). They were captured at 11, 14, and 13 stations in phase four, five, and six, respectively (Supplementary Materials S4).

3.2. Leopard Density Estimates

3.2.1. Survey One

The global learned behavioural (*bk*) response had the best model fit, while neither phase (*T*), sex, nor specific behavioural (*b*) responses improved the null model (Table 2). Based on the *bk*, leopard density was estimated at 1.8 leopards/100 km^2 (*SE* 0.3; *CI* 1.3–2.4; Table 2). While the global behavioural model had the best fit based on the *AICc*, the *CIs* among models were also used to interpret the ecological implications of environmental covariates on detection rates. Based on *AICc* and the *CI*, the trap-specific environmental covariates that improved the model fit of the null model were human abundance, livestock abundance, and elevation (Table 2). Based on the area surveyed, the abundance estimates for survey one was 27 leopards (*CI* 16–45; Table 1). Habitat mask variables of elevation and distance to rivers appeared to best explain leopard density, with a positive relationship to leopard density (Table 2; Supplementary Materials S5).

Table 2. The probability estimate of covariates from the best fit models, with *D* = density/100 km^2, log likelihood (*LL*), and the lower and upper confidence intervals (*CI*) indicating the prediction probability of the effect on λ_0 and σ for survey one (S1) and survey two (S2). Model comparison used the Akaike Information Criterion (*AICc*). σ denotes the detection scale factor, λ_0 denotes the basal encounter rate, and '~1' indicates constant detection parameters. Bold denotes models with a better fit than the null model.

			S1					**S2**				
Model	**Covariate**	**Parameter**	**LL**	**AICc**	**D**	**LCI**	**UCI**	**LL**	**AICc**	**D**	**LCI**	**UCI**
Null	-	~1	−1816.5	3639.6	1.82	1.34	2.47	−596.3	1199.4	1.36	0.9	2.06
Phase	*T*	λ_0, σ	−1814.3	3651.2	1.92, 1.63, 1.94	1.13, 0.93, 1.18	3.29, 2.86, 3.17	−590.5	1208.0	2.16, 1.37, 1.07	0.95, 0.69, 0.5	4.89, 2.71, 2.3
Behaviour	b	λ_0, σ	−1816.5	3641.9	1.84	1.34	2.54	**−594.0**	**1197.6**	**1.74**	**0.96**	**3.13**
	bk	λ_0, σ	**−1794.9**	**3598.7**	**1.78**	**1.3**	**2.42**	**−574.9**	**1159.5**	**1.27**	**0.77**	**2.12**
Sex	sex	λ_0, σ	−1843.0	3697.5	0.92	0.68	1.25	−620.8	1254.1	0.61	0.39	0.95
Environmental covariates												
	Veld Type	λ_0, σ	−1810.6	3630.0	1.86	1.37	2.5	−595.9	1201.3	1.31	0.85	2.02
	Land Use	λ_0, σ	−1816.5	3641.8	1.83	1.35	2.48	−595.9	1201.3	1.32	0.85	2.03
	RAI Livestock	λ_0, σ	**−1808.3**	**3625.4**	**1.79**	**1.32**	2.43	−595.6	1200.9	1.32	0.86	2.03
	RAI Human Activity	λ_0, σ	**−1808.6**	**3626.2**	**1.85**	**1.37**	2.51	−593.2	**1196.1**	**1.29**	**0.83**	**1.99**
	Elevation	λ_0, σ	**−1809.1**	**3627.1**	**1.84**	**1.36**	2.49	−590.7	**1191.1**	**1.80**	**1.21**	**2.68**
	RAI Prey	λ_0, σ	−1813.7	3636.3	1.86	1.38	2.52	−596.0	1201.6	1.31	0.85	2.03
	Distance to Dwelling	λ_0, σ	−1837.0	3682.9	2.02	1.56		−599.0	1207.7	2.05	1.38	3.04
Mask covariates												
Null	-	~1		3639.8	1.82	1.34	2.47	−596,1	1199.0	1.32	0.86	2.03
	Elevation	λ_0, σ	−1814.2	**3637.2**	**1.22**	**0.75**	**1.99**	−589.9	**1189.3**	**0.21**	**0.06**	**0.71**
	Rivers	λ_0, σ	−1814.3	**3637.5**	**5.32**	**2.24**	**12.65**	−596.0	1201.5	1.37	0.88	2.15
	Slope	λ_0, σ	−1815.2	3639.4	1.31	0.78	2.19	−592.5	**1194.5**	**0.21**	**0.04**	**1.33**
	Prey	λ_0, σ	−1815.3	3639.5	1.16	0.58	2.32	−595.7	1201.1	0.80	0.18	3.50
	Land cover	λ_0, σ	−1815.5	3639.9	1.22	0.63	2.39	−590.4	**1190.4**	**1.68**	**0.96**	**2.94**
	Roads	λ_0, σ	−1816.4	3641.8	1.98	1.36	2.89	−596.0	1201.6	1.19	0.53	2.66

3.2.2. Survey Two

The global learned behavioural (*bk*) response also had the best model fit for the survey two analyses (Table 2). Based on the *bk* model, leopard density was estimated at 1.3 leopards/100 km^2 (*SE* 0.3; *CI* 0.8–2.1; Table 2). Behavioural responses (*b*) at the specific site improved the null model and were associated with a higher density estimate and *CIs* (*D* = 1.7; *CI* 0.96–3.13; Table 2) compared to other variables (Table 2). While density was highest in phase four, density estimates were not significantly different among phases (*T*). Sex did not improve the null model. The abundance estimates during survey two was 25 leopards (*CI* 11–47; Table 1). The environmental covariates of the human RAI and elevation improved the null and *b* model, while for the habitat mask, structural features of elevation, slope, and land cover appeared to explain detection rates (Table 2; Supplementary Materials S6).

3.3. Review of Statutory Permits

Between 1975 and 1988, the Nature Conservation Department of the Cape Province (an area now encompassing the Eastern, Western, and Northern Cape Provinces of South Africa since 1994) issued 518 statutory permits to destroy what were considered damage-causing leopards, culminating in the killing of 144 (28%) leopards (Supplementary Materials S2). Additionally, there were 22 reports of illegal leopard-hunting events across the Cape Province (Supplementary Materials S2). However, no leopard-hunting permits or reports (i.e., illegal destruction) were recorded in the Piketberg region and the broader region known as the Swartland. However, between 1989 and 1994, 181 damage-causing animal permits issued to problem animal hunters in the Western Cape included 17 reports around the areas bordering the Swartland to the north of the Piketberg: three in Redelinghuys, two in Het Kruis, and twelve in Citrusdal (Figure 1; Supplementary Materials S2). This demonstrated the presence and destruction of leopards in the areas north of the Piketberg, but none in the Piketberg itself. It is likely that individuals from these nearby populations existing in the Cape Fold Mountains recolonised the Piketberg. No reports of livestock damage caused by leopards were reported between 1985 and 1995, further supporting reports that leopards were absent from the Piketberg mountain and surrounding farmlands in the Swartland. Based on the archive of statutory permits and firsthand accounts, the first report of leopards' reemergence in the Piketberg was recorded in 1995, when a damage-causing leopard was destroyed by Cape Nature [23].

4. Discussion

Our investigation aims to understand how an area that experienced the local extirpation of leopards a century before had been recolonised by the species, reaching the highest densities reported in the region, and what the determinants of this natural recolonisation could be. Reliable population density estimates are key to effective species management. However, density estimates alone are limited to a temporal snapshot and could fluctuate as conditions change. Therefore, understanding factors driving density can provide more insight into population dynamics. Generally, leopard density estimates have been undertaken in protected areas [16,36,42,43]. While protected areas are crucial for carnivore conservation, most leopard habitats in South Africa exist outside protected areas [8,40,44]. Therefore, understanding drivers of leopard densities on privately owned land and various land-use zones is essential to effectively conserve this species.

Using SECR, other studies in the Eastern and Western Cape report estimated ranges of leopard density from ~0.17 to 1.8 leopards per 100 km^2 [10,11,16] (Supplementary Materials S7). Therefore, the Piketberg appears to host a leopard population with some of the highest reported leopard density estimates in the region (~1.8, CI 1.3–2.4 leopards per 100 km^2). Since phases (*T*) did not improve the models, this indicates that the duration of 90 days was sufficient to determine density estimates. Extending survey periods may violate the assumption of surveying a closed population, reducing the scientific rigor of the outputs.

We found that sex did not contribute to explaining density estimates in the Piketberg. This was unexpected since male and female leopards are known to interact differently within their environment [36,40]. This could be because we could not reliably allocate a sex to all of the images obtained (12%), and we generally found more adult males than females for in all camera trap phases. Other camera-based studies also report a male-biased detection ratio, often considered to be the result of camera-shy females or females being more cautious than males [40,45–47]. Furthermore, the highly modified landscape around the Piketberg may limit dispersal opportunities, particularly for males who tend to disperse. As a result, there may be an imbalance, with more males present than females. Additionally, the relatively recent recolonisation of the area could mean that the population is still in the process of stabilising and could be transitioning into a source population and reflect a different sex ratio to extant populations. Female leopards are known to have an important role in how populations are distributed [40], and sex ratios should have a major impact on the population structure, such as infanticide and exclusion competition among males [48]. Therefore, the Piketberg population may not yet be stable since colonisation, in terms of sex ratio, and future monitoring could illuminate if this changes.

The anthropogenic factors of human activity and livestock abundance appeared to predict lower rates of leopard detections. This supports findings elsewhere in the Eastern and Western Cape, where high livestock density areas are avoided by leopards [40,44] but see [49]. This is likely due to high human and livestock density areas being associated with overgrazed and highly transformed areas, offering little if any natural prey [40,44]. High livestock density is also associated with higher human–leopard conflict [40,49]. Livestock production systems often employ carnivore controls, and lethal controls such as leg-hold traps and hunting are commonly used in efforts to reduce carnivore numbers [8,20,50–52]. Indeed, human-caused mortality is considered one of the major drivers of local carnivore population extinctions [6,7,53]. Overall, these factors strongly predict habitat occupancy and population densities outside protected areas, and they highlight the key role privately owned land can contribute to species conservation [7,44,54].

4.1. Drivers of Metapopulation Dynamics/Recolonisation

The Piketberg leopard population appears to be part of a metapopulation, characterised by local extinction followed by recent recolonisation from a source population in the nearby Cape Fold Mountains. This recolonisation occurred in around 1995, prompted by changes in conditions that favoured occupancy once again. We consider four co-occurring factors with varying supporting evidence to explain the leopard recolonisation: (1) land-use transition, (2) fire management regime, (3) the revision of damage-causing animal hunting regulations and management, and (4) increased carnivore–human coexistence.

Firstly, the factors limiting leopard occupation could have diminished as agriculture transitioned from livestock farming toward crops, viticulture, and fruit farming as electrification and the improvement in irrigation technology took hold [55], as this reduced human–carnivore conflicts and increased tolerance, changing the perceptions toward leopards. Additionally, the Piketberg area has seen an increase in nature-based tourism and recreational land uses that promote the value of biodiversity including charismatic species such as leopards and human–wildlife coexistence [55]. Secondly, regularly applied and implemented planned vegetation burns were induced to promote better grazing quantity for livestock [55]. However, constant fires and limit available natural habitats could have contributed toward the local extinction of or avoidance by leopards in the Piketberg. The use of fires set to promote grazing has largely disappeared in the Piketberg mountainous areas over the last few decades as livestock decreased in these sites, and fires are now unplanned, sporadic events [55].

Thirdly, by the mid-1990s, so-called 'vermin'-hunting practices decreased drastically, as the Cape Provincial Administration removed leopards from the vermin list of the Cape Province's Problem Animal Control Ordinance 26 of 1957 in 1968 and stopped subsidising hunters of registered private hunt clubs by the early 1990s [24,25]. In addition, leopards acquired a heightened protection status following the implementation of provincial and national conservation legislation (Ordinance 19 of 1974, CITES, and the National Environmental Management: Biodiversity Act 10 of 2004). The use of indiscriminate carnivore-hunting methods eventually became restricted to permit holders (i.e., poisons, gin traps, night-hunting, blanket species culls, and dog hunting) or were completely prohibited (e.g., coyote getters/gun traps). With the termination of bounties and state-funded 'vermin' hunt clubs, pioneering extension efforts by conservation officials, together with input from conservation interest groups, led to a reduction in predator culling in the Western Cape [41]. The re-emergence of leopards in the Piketberg coincided with the termination of the persistent and extensive hunting of leopards between 1975 and 1994. The statutory permits and hunting reports during this time indicated regular leopard culling in the mountains to the north of the Piketberg, but none in the Piketberg, suggesting the absence of leopards in the area in this period. Therefore, historical predator eradication practices along with other potential human–carnivore conflict practices may have decimated the Piketberg leopard population and acted as a barrier preventing leopard dispersal from the surrounding mountains, until the termination of these activities in the early 1990s, allowing the dispersal and re-occupation of the area afterward.

Overall, the reduction in lethal carnivore controls and lethal state-management practices (i.e., predator culling) and a change in landowner attitude toward wildlife and carnivores coincided with the re-emergence of leopards in the Piketberg region in around the mid-1990s and appears to have played a determinant role in the recolonisation.

4.2. Species Management Implications and Policy

Natural recolonisation remains relatively undocumented in the South African context, and to our knowledge, this is the first recorded naturally recolonised leopard population in South Africa. Globally, however, natural recolonisation has been reported [56–58]. These were successful due to supportive public opinion toward predators, the implementation of national and international legislations for large carnivore conservation, and structural changes in agriculture, leading to widespread rural human exodus and farm abandonment or changed management practices [59]. Some notable examples include the recolonisation of wolves (*Canis lupus*) to their historic ranges within several human-dominated landscapes in Central and Western Europe [60] and the iconic recolonisation case that followed the meltdown of the nuclear reactor in Chernobyl (1986). In the Chernobyl Exclusion Zone, ecological monitoring showed the return of locally extinct species, such as large mammals (e.g., *C. lupus* and *Alces alces* [61]) and raptors (e.g., *Clanga clanga* and *Haliaeetus albicilla* [62]), reflecting a decreased human threat to local species.

The recolonisation of the Piketberg leopard population is encouraging and illustrates the powerful role that state policy and land management plays in opportunities for rewilding and recolonisation where remnant habitats exist. This study also highlights the disastrous impact that the incentivised and deliberate culling and lethal control of a species has had on its persistence in the Western Cape landscape.

Despite this positive ecological response, potential threats loom on the horizon. Emerging political and industry pressures in the agricultural sector, as evidenced by the push to reinstate vermin hunt clubs and draft policies supporting the incentivised hunting of so-called damage-causing individuals, raise concerns about the sustainability of the recolonised leopard population (Cooperative agreement between the Predator Management Forum and Cape Nature Conservation Board, 2013; South African National Government Department of Forestry, Fisheries and the Environment, 2023; https://www.gov.za/sites/default/files/gcis_document/202309/49319gon3887.pdf, accessed on 22 September 2023). The historical impact of incentivised and deliberate culling on leopard persistence in the Western Cape landscape further emphasises the need for caution in employing these methods in wildlife management [41].

Considering the ongoing global loss of biodiversity, the successful recolonisation of leopards in Piketberg serves as a timely reminder that, with informed and effective conservation strategies, nature can rebound even in the face of past human-induced challenges. The conservation implications are clear. Achieving balanced human–carnivore coexistence is paramount, necessitating the adoption of alternative non-lethal practices and mitigation actions [52,63–65]. Intensive conservation efforts, including the establishment of wildlife corridors and minimising human-caused mortality are essential for promoting leopard dispersal and ensuring long-term population viability [21,44,66,67]. Continued research, advocacy, and support from management agencies, such as Cape Nature and alike in the state apparatus, are vital for sustaining and expanding the successes observed in the recolonisation of leopards within their historical range.

Together, fewer intentional burns, changed land use, increased tolerance, and the termination of the incentivised leopard extirpation through state-sponsored bounties and subsidised vermin-hunting efforts coincided with the recolonisation of the study area. Finally, the return of leopards in their historical range ought to be supported by management agencies and conservation actors through ongoing evaluations and research, extension services and education work, and ongoing advocacy for greater tolerance and coexistence support with these top-trophic species.

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