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Abstract

Large carnivores are in decline globally. The leopard's (*Panthera pardus*) adaptability enabled its survival as the last remaining apex predator in the Western Cape, South Africa. Limited suitable habitat and anthropogenic activity imperil the continued survival of leopards, yet density estimates are lacking in the Western Cape, especially across unprotected areas We employ the flexible modelling environment of Just Another Gibbs Sampler (JAGS) to implement a Bayesian spatial capture-recapture (SCR) model and generate the first density estimate for the leopard population in the Boland Mountain Complex using a dataset collected in 2010 – 2011. Leopard density was estimated at 1.69/100 km^2 (95% CI=1.4-1.99) with adult female leopards occurring at a higher density (0.93/100 km^2 (95% CI=0.64-1.18)) than males (0.76/100 km^2 (95% CI=0.62-0.90)). Our modelling shows that males have more extensive ranges than females, increasing their susceptibility to anthropogenic threats which are generally more abundant at the study area's periphery. Tailored conservation efforts are recommended in conjunction with an up-to-date leopard population density reassessment. The JAGS approach to SCR also enabled a detailed investigation of animal distribution and movement, and provides a reliable methodology to monitor population trends.

Introduction

The first written records of the leopard (*Panthera pardus*) in southern Africa originate from the Cape, dating to the early 1600s. At the time, the southwestern tip of Africa was also inhabited by African elephant (*Loxodonta africana*), African buffalo (*Syncerus caffer*), hippopotamus (*Hippopotamus amphibius*), black rhinoceros (*Diceros bicornis*), spotted hyaena (*Crocuta crocuta*), and lion (*Panthera leo*) (Boshoff et al., 2016; Skead et al., 2011). All of these, except for the leopard, have since been extirpated in the Western Cape (Kerley et al., 2003). Despite extensive habitat loss, direct persecution, and reduction in prey numbers, leopards have managed to persist in the mountains of the greater Western Cape region and now fill the role of apex predator in this ecosystem (Swanepoel et al., 2016; Swanepoel et al., 2013).

The leopard is listed as Vulnerable both on the IUCN Red List (Stein et al., 2020), and the Red List of Mammals of South Africa, Swaziland, and Lesotho (Swanepoel et al., 2016). Leopards face numerous threats to their survival including human-induced mortality and habitat fragmentation, and these are compounded by low population densities (Jacobson et al., 2016; Swanepoel et al., 2015). Leopards living outside of protected areas experience greater exposure to anthropogenic threats (Swanepoel et al., 2015). However, despite the importance of private land for leopard survival, there is a paucity of information on leopard populations, threats to leopards, and the effectiveness of conservation measures in these areas (Balme et al., 2014; Jacobson et al., 2016; Swanepoel et al., 2013).

Reliable estimates of population size, density, and distribution, and trends in these at regional and local scales are necessary for governments and land managers to take informed management action. An adequate understanding of the anthropogenic and ecological factors that influence the distribution of this species within their environment is also vital for adaptive management strategies. However, leopards in the Western Cape are arguably more challenging to effectively monitor than leopard populations in other regions of Southern Africa because of their large home ranges, low population densities, and the fragmented and inaccessible landscapes they occupy (Martins & Harris, 2013; Martins, 2010; Swanepoel et al., 2013). The use of camera trapping as a survey tool for medium-to-large terrestrial mammals, especially rare and elusive species, has become increasingly common over recent years (O'Connell et al., 2011).

Capture-recapture methods (also known as mark-recapture or capture-mark-recapture) have been used to estimate the size of animal populations including large carnivores for many years; the first software package for this analysis, CAPTURE (Otis et al., 1978) was created in 1978. Early methods did not incorporate the spatial component in the data and spatial capture-recapture (SCR) models first appeared in 2004 (Efford et al., 2004). A major source of heterogeneity in capture probability is due to individual animal's movement patterns and trap locations, i.e. the probability of capture in a specific trap depends on its location relative to the movement of the animal (Efford, 2004). SCR models incorporate this spatial element. In addition, leopards exhibit sex-specific differences in space-use and behaviour, with the home range of a single territorial male overlapping with smaller home ranges of several females (Fattebert et al., 2016; Sandell, 1989). These differences in space-use and movement ranges between the sexes will be reflected in differences in encounter probability with camera traps (Sollmann et al., 2011) but separate density estimates for sexes are seldom ascertained for leopards. Location of cameras is also a likely source of capture heterogeneity (Royle et al., 2009a; Sollmann et al., 2011).

Despite advances in SCR modelling, many studies lack sufficient precision for long term monitoring (Green et al., 2020). To improve accuracy and precision in the estimates, we sample a large study area to increase multiple site photographic captures and use the flexible modelling environment of Just Another Gibbs Sampler (JAGS) to implement a Bayesian SCR model. This model accounts for patchy habitat coverage and heterogeneity in capture probability due to sex and trap locations to obtain reliable density estimates of the leopard population in the Cape Fold Mountains in the Western Cape, South Africa. Our study, while based on data collected 10 years ago, provides important insights into leopard distribution in an understudied montane area comprised of protected and non-protected land, and generates a robust baseline population density estimate which will allow assessment of conservation progress through future surveys using the same methodology.

Materials and Methods

Study area

The study area is located in the southwestern tip of South Africa and covers 2,500 km^2 of the Cape Fold Belt Mountain chain (Figure 1). The core of the study area consists of six protected areas (Limietberg, Jonkershoek, Hottentots-Holland, Kogelberg, Helderberg, and Steenbras nature reserves) managed by two statutory conservation bodies (CapeNature and City of Cape Town). Collectively, this area is referred to as the Boland Mountain Complex (BMC), an inscribed World Heritage Site - one of eight sites which collectively comprise the Cape Floristic Region (United Nations Educational Scientific and Cultural Organization, 2021). The study area also overlaps with the UNESCO Cape Winelands and Kogelberg Biosphere Reserves. A significant proportion of the study area is located on private reserves, farms, and state or municipal owned water catchment areas which are adjacent to the protected areas and also regarded as suitable leopard habitat. Although the core of the mountain reserves remains fairly pristine, the edges are heavily impacted by habitat alteration and urbanisation. The dominant land use surrounding the study area is agriculture (specifically viticulture and fruit production), forestry, urban and semi-urban development, with a low level of small-scale livestock farming.

The area has a Mediterranean climate and a winter rainfall regime with mean annual precipitation in the majority of the study area averaging between 530 - 3,000 mm (Keeley et al., 2011; Mucina & Rutherford, 2006). Geologically, the area primarily consists of Table Mountain Sandstone of the Cape Supergroup (Bradshaw & Cowling, 2014). The terrain is characteristic of the Cape Fold Belt Mountain chain with high mountain peaks, rugged slopes, deeply incised valleys, undulating valleys, drainage lines, and rivers. Altitude ranges from sea level to 1,750 m asl (Bradshaw & Cowling, 2014). Some of the ranges within the BMC have an extreme topography with few to no foothills and rising directly from the valley floor, resulting in a large proportion of barren rock faces and steep cliffs.

Camera trap survey design and camera placement

Ideally, sufficient camera traps are deployed to sample the entire target area in one survey, but this was not feasible due to the size of the study area and a limited number of camera traps. The target area was thus divided into two sub-sections (northern and southern; Figure 1) and surveyed separately. This is an acceptable alternative as the closed population assumption was satisfied in congruence with spatial and temporal considerations of the population (Foster & Harmsen, 2012).

Resident female leopards of breeding age have the smallest home ranges (Fattebert et al., 2016; Mizutani & Jewell, 1998). Using localised home ranges estimates, we regarded the minimum home range of a female leopard as 50 km^2 (Martins, 2010). The 2,500 km^2 study area was thus divided into a 50 km^2 grid system. Cuddeback® (Cuddeback, Green Bay, Wisconsin USA) Capture and Expert strobe-flash camera traps were deployed at 92 locations, with each 50 km^2 block of suitable habitat containing at least one paired camera station, plus a further single camera station in most cases. Camera stations were spaced at least 2 km apart from each other. Extreme topography, inaccessible mountainous terrain, and high theft risk locations precluded the placement of cameras in some areas and resulted in a few gaps in coverage. The flexibility of SCR methods can successfully produce robust estimates when uneven coverage in the trap array occurs (Borchers & Efford, 2008; Royle et al., 2009b).

Camera trap placement was optimised for leopard detection. Camera traps were placed on well-used game paths, hiking trails, vehicle tracks, and drainage lines, at a standardised height of 30 cm above ground level. Camera traps were placed perpendicular to the trail to obtain a full lateral body image of a passing animal. A leopard's rosette patterns are asymmetrical on either side of the body, and thus paired cameras allowed for a simultaneous left and right flank images to facilitate accurate individual identification. Camera traps at paired stations were off-set slightly to avoid the simultaneous strobe flashes causing a white-out in the images. All camera traps took a single image per trigger. The cameras had a time delay of one minute between sequential triggers. Cameras were serviced every 6 - 8 weeks to change batteries and download images. The northern (1 July 2010 - 7 November 2010) and southern (15 December 2010 - 23 April 2011) sections of the study area were surveyed in rapid succession. Both surveys ran for a total of 130 days each. The survey length aligns with leopard's slow life-history and large home range size in the Cape, thus generating sufficient photographic captures to improve the precision of estimates while satisfying the population closure assumption (Dupont et al., 2019).

Statistical Analysis

Individual leopards were identified based on their unique rosette patterns, and sex was determined by morphological characteristics such as neck girth and external genitalia. Cubs and unidentifiable leopard images were discarded from the dataset. Leopard population density was estimated using the Bayesian SCR method. The model p0(sex).sigma(sex), where p0 denotes the probability of capture when the distance between the animal's activity centre and the camera is zero and sigma is the ranging scale parameter, was implemented in the programme JAGS accessed through the programme R, version 4.0.4 (R Development Core Team, 2021) using the package RJAGS (http://mcmc-jags.sourceforge.net). The habitat mask was derived by first generating a set of grid points with 500 m separation using 'Fishnet' tool in ArcGIS Desktop Version 10.0 (ESRI, Redlands, CA). This was then clipped with a leopard habitat shape file beyond which any animals with an activity centre outside the habitat mask had a negligible probability of being captured. Any non-habitat patches (i.e., areas where leopards will not cross on a daily basis, specifically urban, semi-urban and agricultural transformed land) were also excluded from the mask (see Figure 4). The size of the habitat mask was 14290 pixels (3572.5 km^2).

In data augmentation, M was set to 200 - larger than the largest possible population size (i.e., the number of activity centres). The centroid of capture locations of individual animals caught were used as the starting values for activity centres, ensuring these occurred in suitable habitat as defined in the habitat mask. Three MCMC (Markov Chain Monte Carlo) chains with 60,000 iterations, a burn-in of 1,000, and a thinning rate of 10 were implemented. This combination of values ensured an adequate number of iterations to characterise the posterior distributions. Chain convergence was checked using the Gelman-Rubin statistic (Gelman et al., 2004), R-hat, which compares between and within chain variation. R-hat values below 1.1 indicate convergence (Gelman & Hill, 2006). The approach of Royle et al. (2013a) was used for the model goodness-of-fit test, calculating three statistics, all using Freeman-Tukey discrepancies: individual animal by camera station capture frequencies, aggregating the binary daily capture data by animals and camera stations (FT1); individual animal capture frequencies, aggregating for each animal (FT2); camera station animal capture frequencies, aggregating for each camera station (FT3).

In case the p0(sex).sigma(sex) model fit was inadequate with $P<0.05$ for the three Freeman-Tukey discrepancies, we assessed capture heterogeneity among camera stations by plotting histograms of observed and posterior predictions for the total number of camera stations visited by leopards, the maximum visits per camera station, the maximum detections for one animal per one camera station, and the maximum detections per animal. We then fitted the model p0(sex+trap).sigma(sex) using the above procedure.

Posterior distributions of adult male, female, overall population density and abundance, and male and female ranging parameters were generated from the model. Posterior locations of individual leopard activity centres were mapped, and an animal density map (individuals / km^2) was produced by modelling the movement of animals around activity centres. Male and female home range sizes were estimated based on the half-normal detection model where 95% of the animal's detectable "activity" occurs within 2.45 x sigma of the activity centre (Royle et al., 2013b).

Results

The study accumulated 11,343 trap nights across 92 camera trap stations. Excluding repeat detections at the same location by same individual within a 24 hour occasion, there were 312 adult leopard detections at 71 camera trap stations (42 individual adults with 21 males, 18 females and 3 unknown sex) (see Table S1 for additional survey results).

Although the p0(sex).sigma(sex) model converged, the Freeman-Tukey discrepancies had $P<0.05$. Further analysis (see methods) revealed capture heterogeneity among camera stations. The model p0(sex+trap).sigma(sex) fitted well to the data (FT1 P=0.43, FT2 P=0.34, FT3 P=0.34) and R-hat values for all model parameters were below 1.1 (see Figure S1).

The posterior probability for adult male movement parameter sigma being greater than the adult female sigma was one (Table 1, Figure 2). Adult female density (0.93 (95% CI=0.64-1.18) individuals/100 km^2) was larger than adult male density (0.76 (95% CI=0.62-0.90) individuals/100 km^2) with a posterior probability of 0.84 (Figure 3). Adult female density estimate was less precise (CV=15.07%) than adult male density estimate (CV=10.3%), and therefore accounted for a larger portion of the uncertainty in the population density estimate (CV=9.42%). The adult female to male sex ratio was 1.24 (95% CI=0.83-1.71). The estimated leopard population density was 1.69 (95% CI=1.4-1.99) individuals/100 km^2 and abundance 60 (95% CI=50-71) individuals. The species displayed a patchy distribution across the study area (Figure 4). Adult females were generally captured multiple times in a small area, so there was greater certainty in their activity centres. The males, though, were captured less often or over a wider area (Figure 4, Figure S2). The estimated adult male leopard average home range radius was 12.5 (95% CI=11.37-13.65) km and range size 491 (95% CI=406-585) km^2. The average home range radius of adult female leopards was 5.78 (95% CI=4.97-6.69) km with range size 105 (95% CI=78-141) km^2.

Discussion

In this study, we used the flexibility of JAGS to implement SCR models to estimate densities of a leopard population occurring in the patchy habitats of the Cape Fold Mountains. We accounted for trap heterogeneity in capture probability and assessed model fit using Freeman-Tukey discrepancy measures. The Bayesian model outputs also provided insights into population structure, individual animal activity centres, distribution, movement range and home range size.

Leopards in the Cape Fold Mountains have been shown to exist at comparatively low densities (Table 2) and utilise very large territories (Devens et al., 2018; Martins, 2010). Compared to other leopard populations in the Western Cape, the BMC has one of the highest leopard densities within the Cape Fold Mountains distribution range. Only Langeberg has a slightly higher estimated density but the 95% confidence interval is much wider (1.89/100 km^2, 95% CI=0.89–2.50) (Devens et al., 2018). However, the age of this study's dataset must be considered when comparing findings to more recent estimates.

Despite the population's relatively high density compared to other populations in the Western Cape, leopards are susceptible to a wide array of threats. Low leopard densities, limited suitable habitat, fragmented connectivity between leopard populations, and an increasing human population augment the vulnerability of leopards in the BMC (Swanepoel et al., 2013). Within the BMC it was recently shown that a wide range of animal species are affected by illegal wire snare poaching on private property (Nieman et al., 2019b). Small antelope such as common duiker (*Sylvicapra grimmia*), Cape grysbok (*Raphicerus melanotis*), klipspringer

(*Oreotragus oretragus*), and grey rhebuck (*Pelea capreolus*), as well as Cape porcupine (*Hysrix africaeaustralis*) are highly sought-after hunted species with high off-take rates (Nieman et al., 2019b). These small antelope and porcupine form the primary prey base (62% relative biomass) of leopard in the study area (Mann et al., 2019). Mann et al. (2019) also highlight that future changing aridity may force cultivated areas to creep up the slopes into cooler and higher land in the BMC region, thus reducing habitat and prey availability for leopard. Nieman et al. (2020) recorded the presence of feral dogs in packs of up to 18 within the BMC. It is not certain to what extent these dogs exert pressure on the prey base, increase disease transmission, or pose a threat to leopards through direct conflict. Biological harvesting for traditional healing purposes is an additional suspected threat with a high incidence of leopard skins and body parts possessed by traditional healers in the Boland region (Nieman et al., 2019a). Unfortunately, respondents were not willing to reveal the origin of the skins/body parts, so a direct local off-take connection could not be made (Nieman et al., 2019a).

Our study also provided important insights on the spatial ecology of leopards in the Cape. The estimated average home range radius of adult male leopards in the BMC was over twice the radius of adult female leopards. The protected areas at the core of the BMC are almost exclusively enveloped by transformed lands and are thus seen as biodiversity refugia. Males with their larger home ranges and greater need for wide dispersal when establishing home ranges are more likely to experience negative edge effects as they venture into private land at lower altitudes where multifaceted anthropogenic threats are present (Balme et al., 2010; Woodroffe & Ginsberg, 1998). Carnivores alter their activity patterns or shift the way they utilise space in response to entering a perceived 'landscape of fear' where humans assume the role of apex predator (Stillfried et al., 2015; Suraci et al., 2019; Valiex et al., 2012). We suggest future studies assess how anthropogenic activity affects leopard activity patterns and behaviour in the BMC.

Management implications

Conservation measures aimed at reducing illegal hunting are urgently needed in the BMC. These include educating landowners on the importance of communication with staff about the repercussions of snaring, removing materials that can be opportunistically fashioned into snares, and conducting effective snare removals (Nieman et al., 2019b). Intensified but carefully considered law enforcement is also required (Nieman et al., 2019b). However, these approaches do not ameliorate the socioeconomic drivers of illegal hunting. In illegal hunting hotspots, education programmes aimed to upskill workers and improve employability should be trialled.

In addition, due to the age of this dataset and the vulnerability of the population, an urgent leopard population reassessment in the BMC utilising a JAGS based SCR approach is advised to compare current density estimates with this baseline estimate. Standardised monitoring of core populations is recommended on a periodic basis to monitor population dynamics (Nichols & Williams, 2006). Detected shifts in a population's stability require investigation into factors provoking population change and the application of tailored and timely conservation management (Nichols & Williams, 2006). Movement corridors between the BMC and adjacent leopard habitats should be ascertained and protected to ensure genetic viability of this potentially isolated population.

As habitats for leopards in the Cape become increasingly fragmented, the concept of a conservation landscape (that is, a network of protected areas separated and surrounded by alternative land use) provides a more effective framework for conservation actions (Wiens, 2009). Incorporating a socio-ecological approach to conservation landscape management is vital (Palomo et al., 2014). Monitoring at the spatial scale of individual reserves are needed to help ensure BMC and other core areas can continue to function as source populations and refugia in the future.

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Data available on request from the authors.

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Table 1. Estimates of leopard sex-specific and overall population Bayesian spatial capture recapture model parameters in the Boland Mountain Complex, Western Cape. Sigma is the ranging scale parameter.

	Density (individuals/100 km^2)	Population Size	Sigma (in km)
Adult females	0.93 (95% CI 0.64–1.18)	36 (95% CI 25–45)	2.36 (95% CI 2.03–2.73)
Adult males	0.76 (95% CI 0.62–0.90)	28 (95% CI 23–33)	5.1 (95% CI 4.64–5.57)
Adults overall	1.69 (95% CI 1.4–1.99)	60 (95% CI 50–71)	N.A.

Table 2. Summary of leopard density estimates in the Western Cape based on the SCR method.

Study	**Region and Details**	**Density estimate /100 km^2**	**Method (package)**
This study	Boland Mountain Complex	1.69 (95% CI=1.4–1.99)	SCR-Bayesian (JAGS)
(Mann et al., 2020)	Little Karoo	1.26 (SE ± 0.25)	SCR-Maximum Likelihood (secr)
(Devens et al., 2018)	Agulhas	0.69 (95% CI=0.39–1.28)	SCR-Bayesian (SPACECAP)
	Baviaanskloof	0.24 (95% CI=0.19–0.36)	
	Garden Route	0.96 (95% CI=0.36–1.49)	
	Langeberg	1.89 (95% CI=0.89–2.50)	
(Devens et al., 2021)	Langeberg	0.50 (95% CI=0.39–1.09)	SCR-Maximum Likelihood (secr)
		1.89 (95% CI=0.89–2.50)	SCR-Bayesian (SPACECAP)
	Garden Route	0.38 (95% CI=0.17–0.87)	SCR-Maximum Likelihood (secr)
		0.96 (95% CI=0.52–1.49)	SCR-Bayesian (SPACECAP)

	Overberg	0.17 (95% CI=0.06–0.48)	SCR-Maximum Likelihood (secr)
		0.69 (95% CI=0.39–1.28)	SCR-Bayesian (SPACECAP)

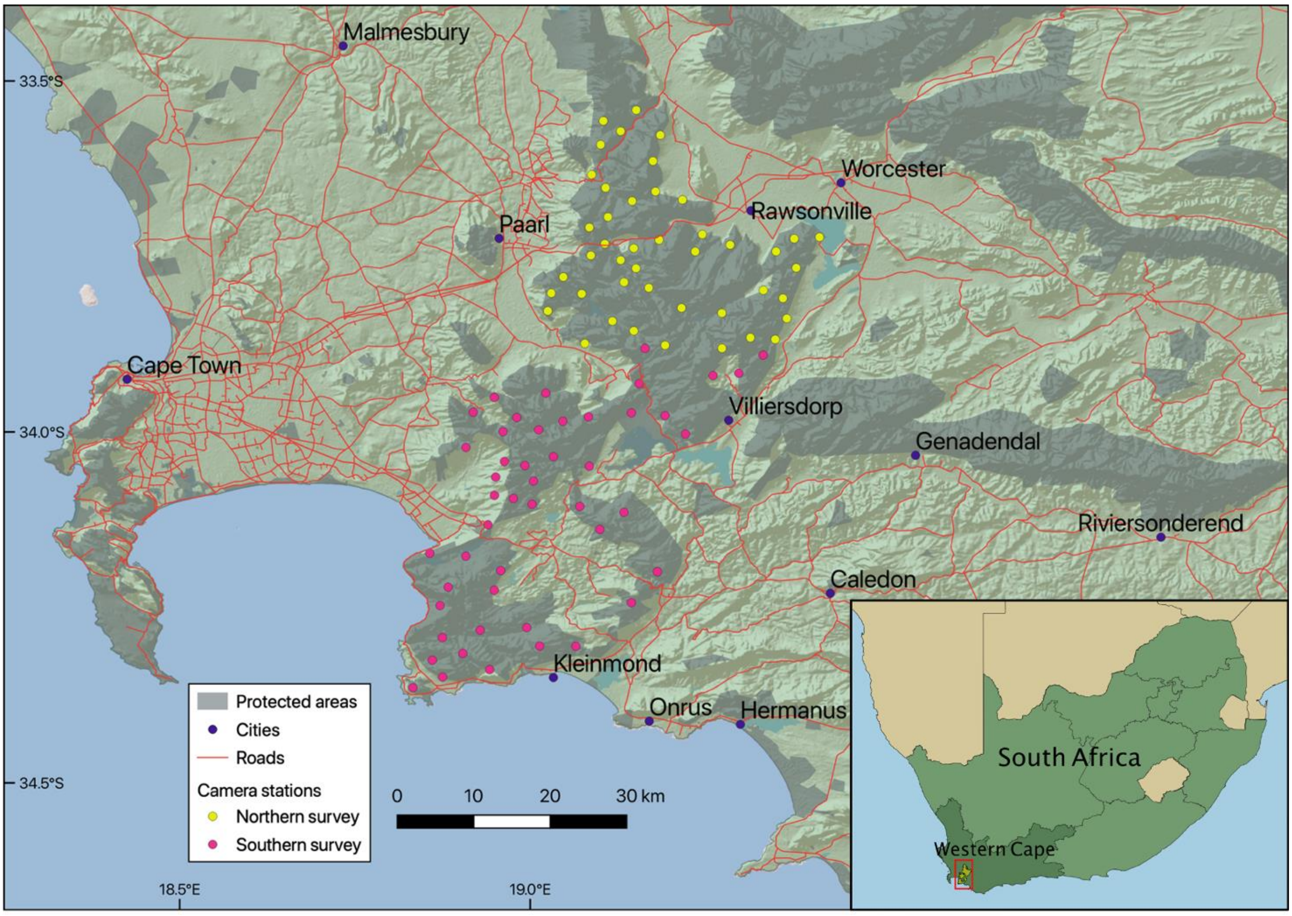


Figure 1. The study area within the Boland Mountain Complex, South Africa. Protected areas (grey shading) encompass the majority of the study area.

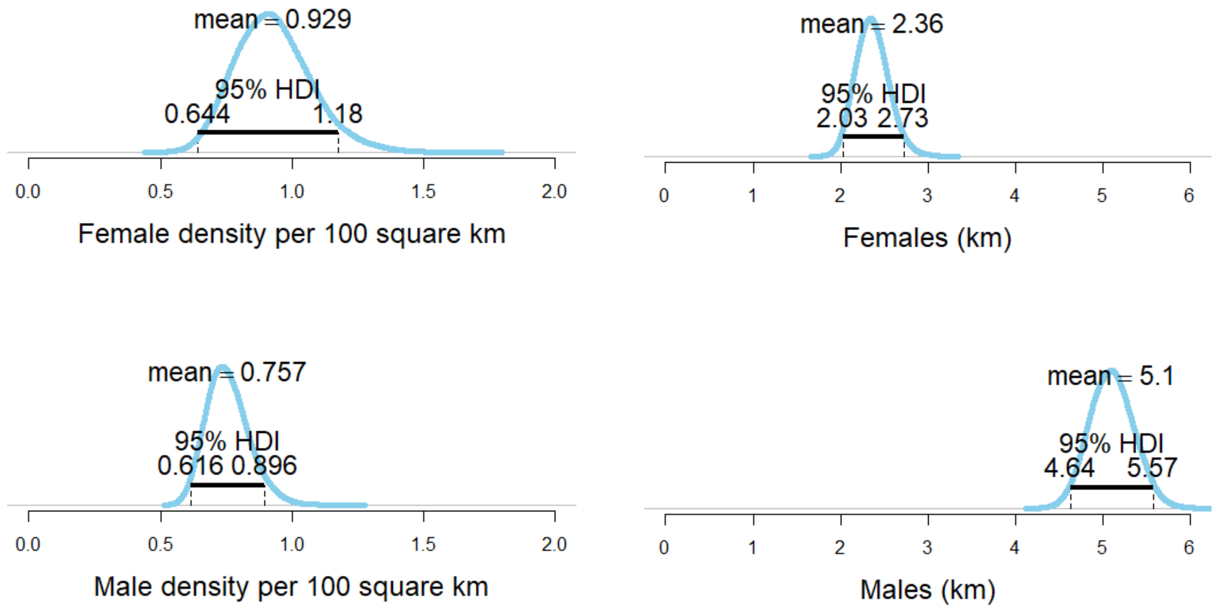


Figure 2. Left: Adult female and male density posterior distributions. Right: Adult female and male sigma posterior distributions, Boland Mountain Complex, Western Cape.

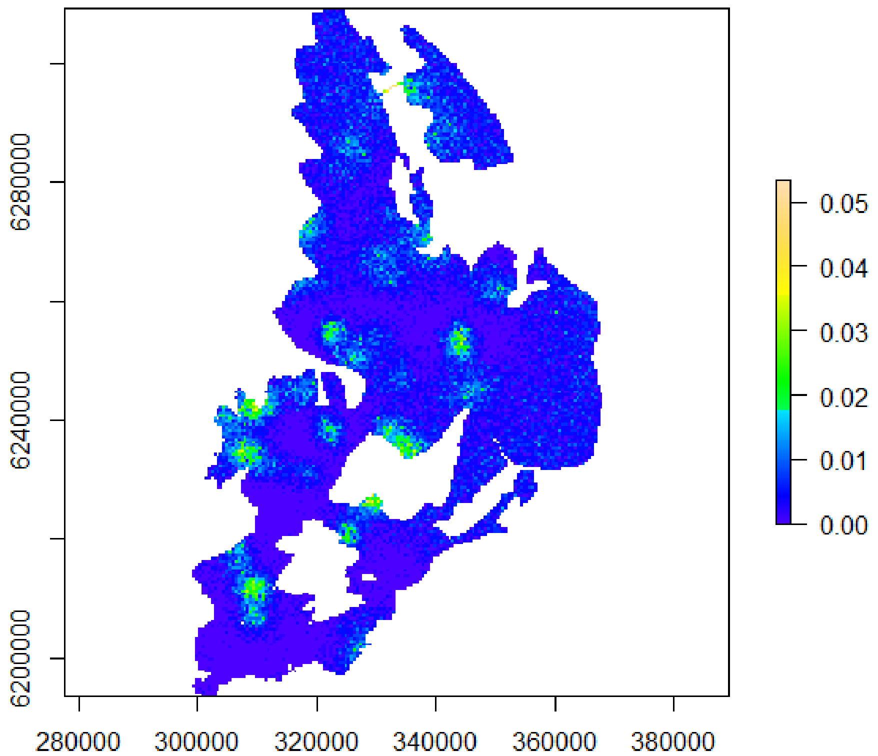


Figure 3. Expected density of individual leopards (individuals/km^2) predicted from the Bayesian SCR model, Boland Mountain Complex, Western Cape. The map coordinate system is UTM (x and y axis in meters).

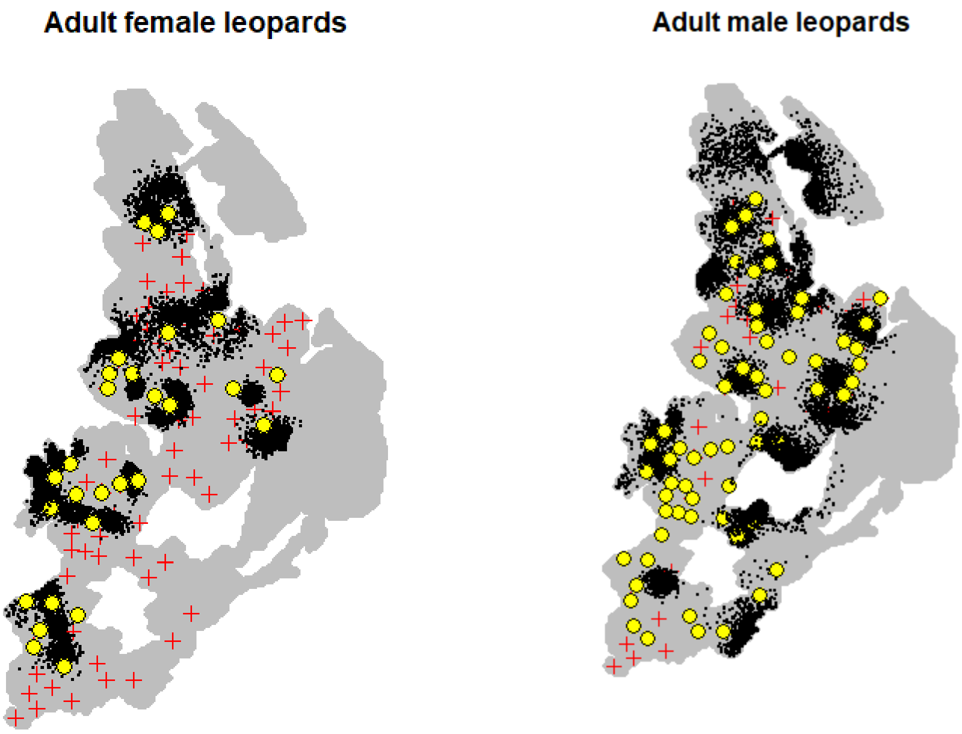


Figure 4. Activity centre posterior distributions (black dots representing uncertainty in animal activity centres); capture locations (yellow circles); and camera trap locations (red crosses) for all recorded adult females (left) and adult males (right) in the Boland Mountain Complex, Western Cape.

Supplementary Materials

Assessing the status of leopard in the Cape Fold Mountains using a Bayesian spatial capture-recapture model in Just Another Gibbs Sampler

Rajan Amin, Anita Wilkinson, Kathryn S. Williams, Quinton E. Martins, Jeannie Hayward

Table S1: Summary of the camera survey conducted in the Boland Mountain Complex between 1 July 2010 and 23 April 2011.

	Number
Survey effort (operational trap nights)	11,343
Camera stations	92
Number of stations where leopards were detected	73 (79%)
Total leopard detections (including sub-adults and cubs)	371
Total adult leopard detections (excluding repeat triggers at the same station within a 24 hour period)	312
Leopard detections in Northern section (44 stations)	147
Leopard detections in Southern section (48 stations)	165
Individual adult leopards identified total	42
Individual leopards identified in Northern section (44 stations)	24
Individual leopards identified in Southern section (48 stations)	23

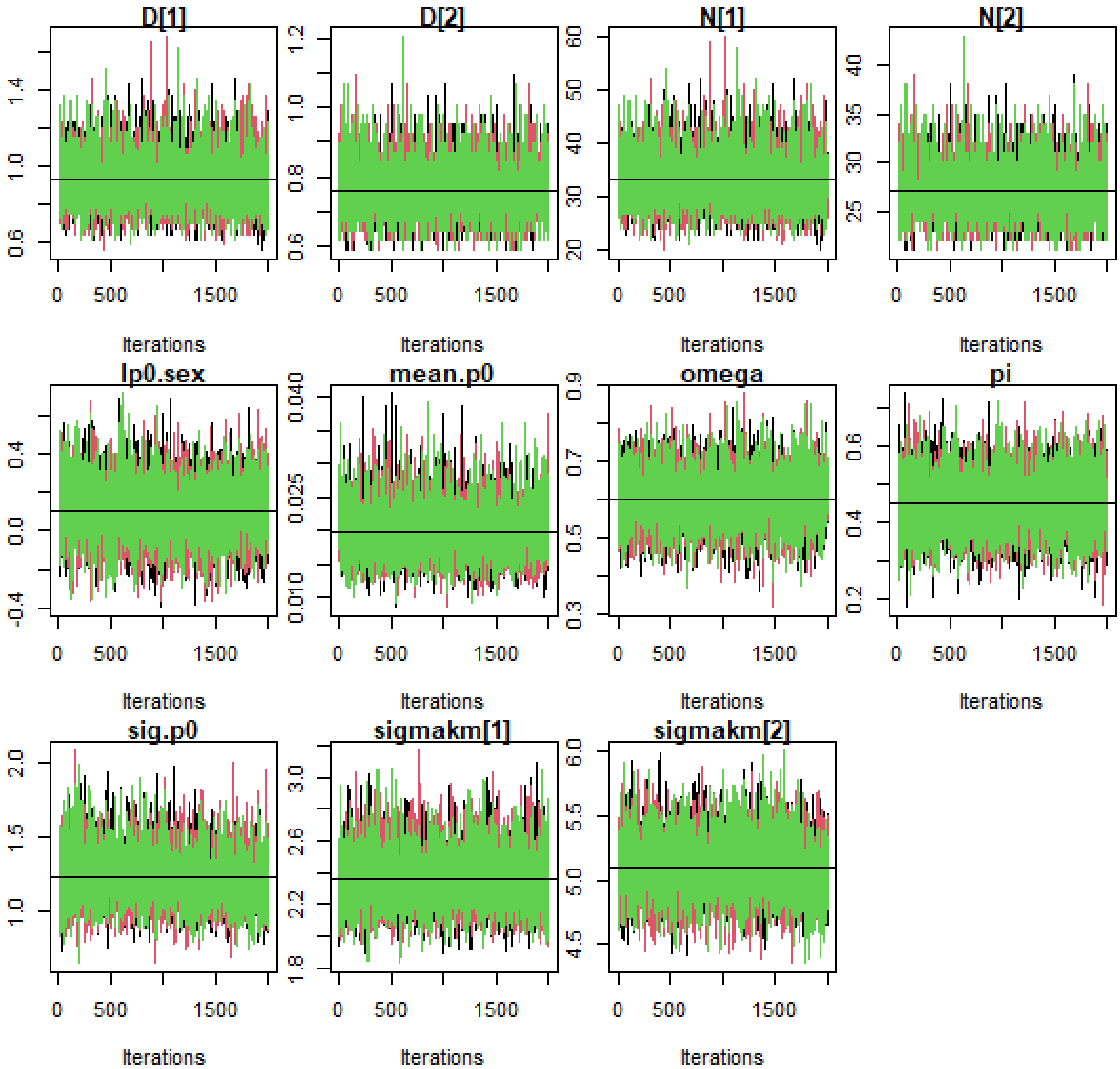
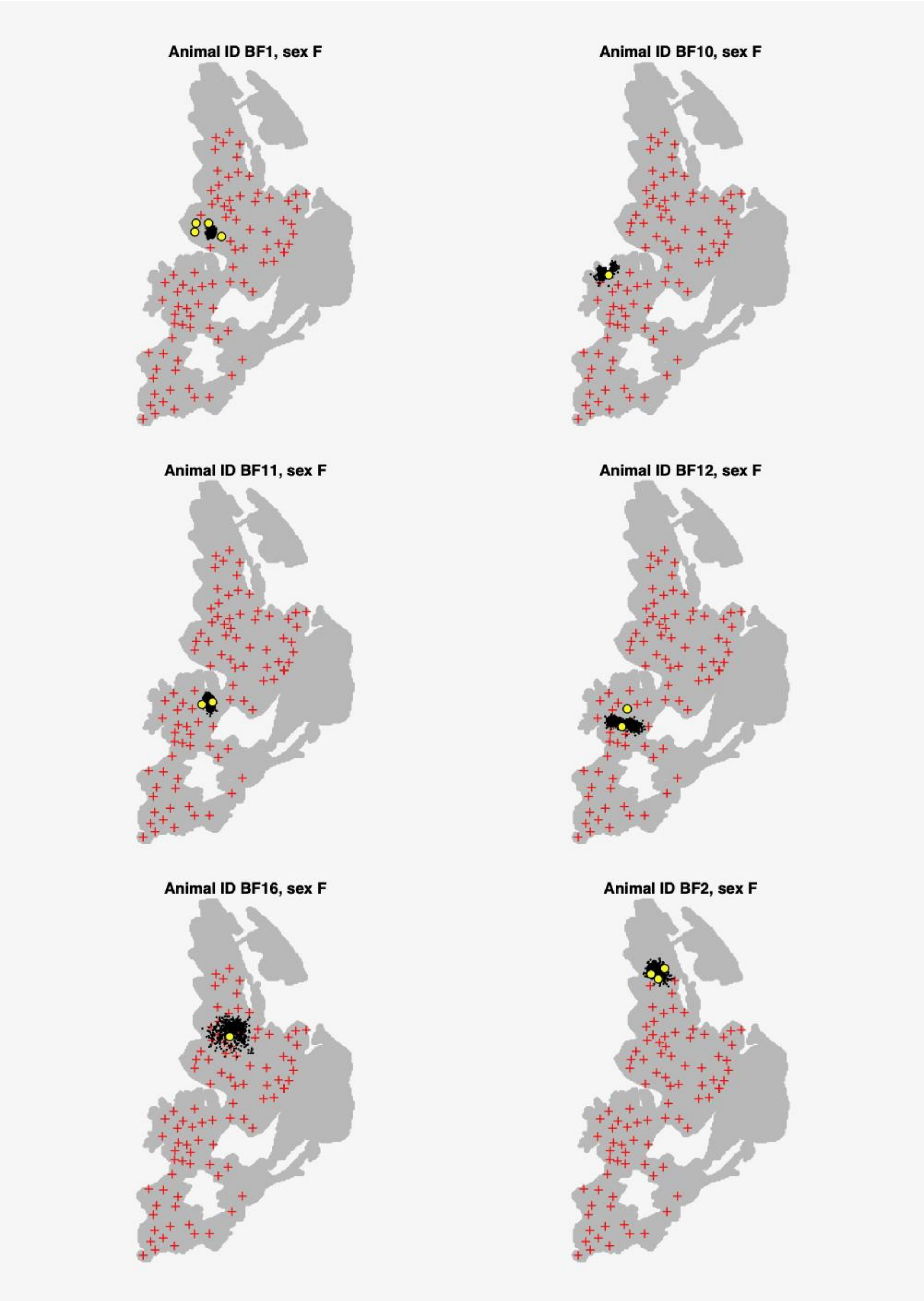


Figure S1. Model [p0(sex+trap).sigma(sex)] diagnostic trace plots.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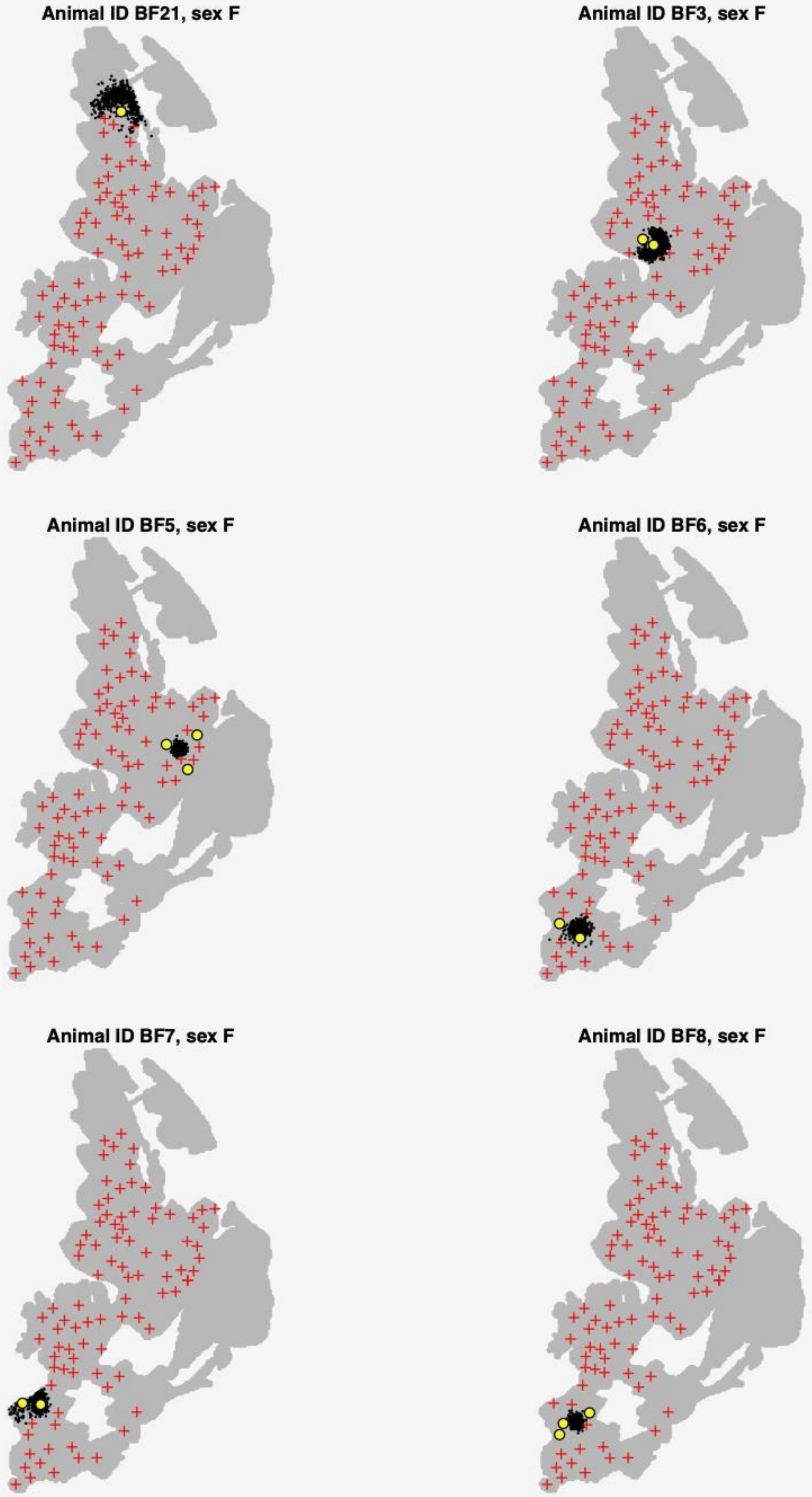
Animal ID BF12, sex F
Animal ID BF16, sex F
Animal ID BF2, sex F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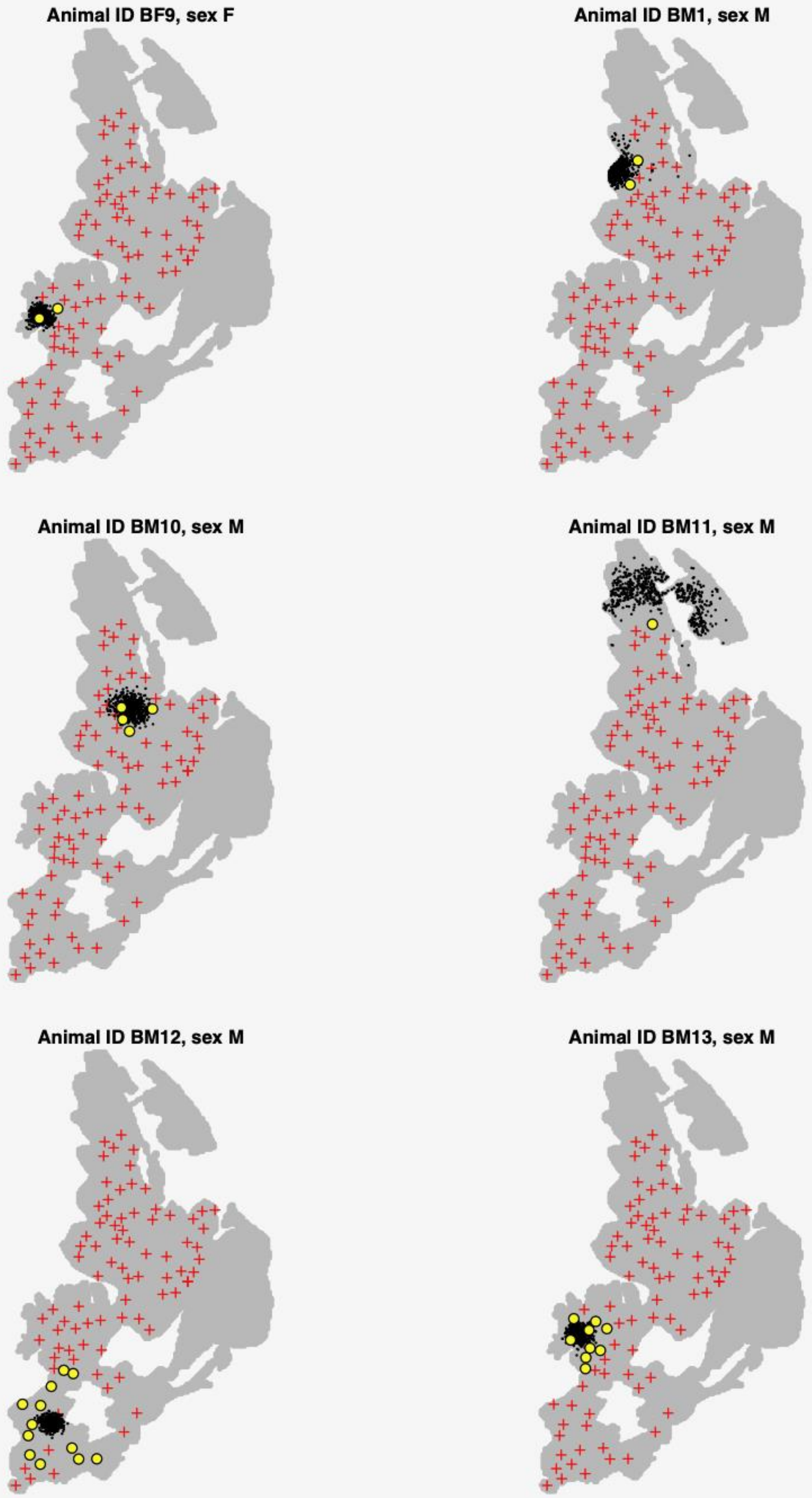
Animal ID BF6, sex F
Animal ID BF7, sex F
Animal ID BF8, sex F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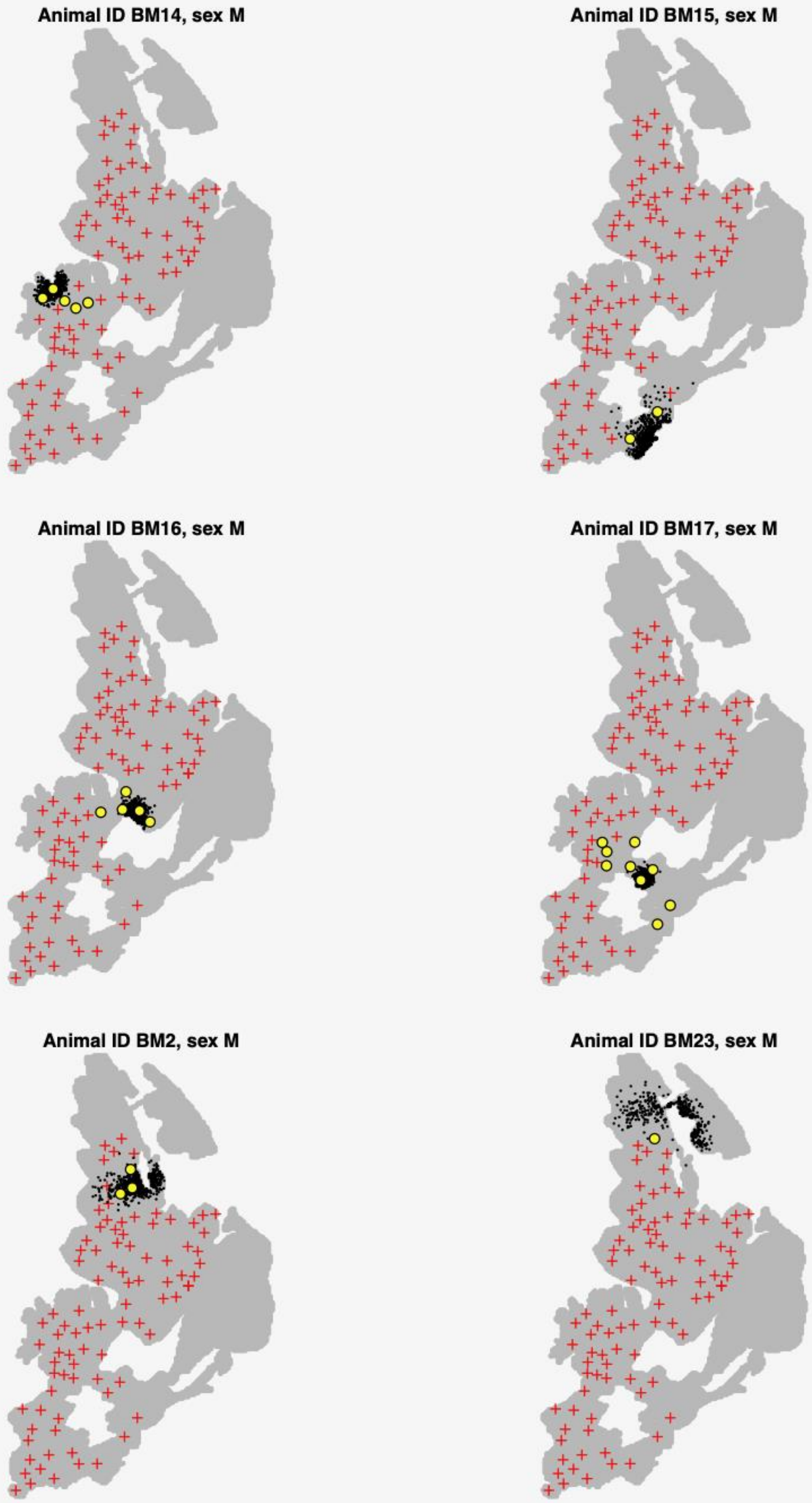
Animal ID BM1, sex M
Animal ID BM10, sex M
Animal ID BM11, sex M
Animal ID BM12, sex M
Animal ID BM13, sex M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Animal ID BM17, sex M
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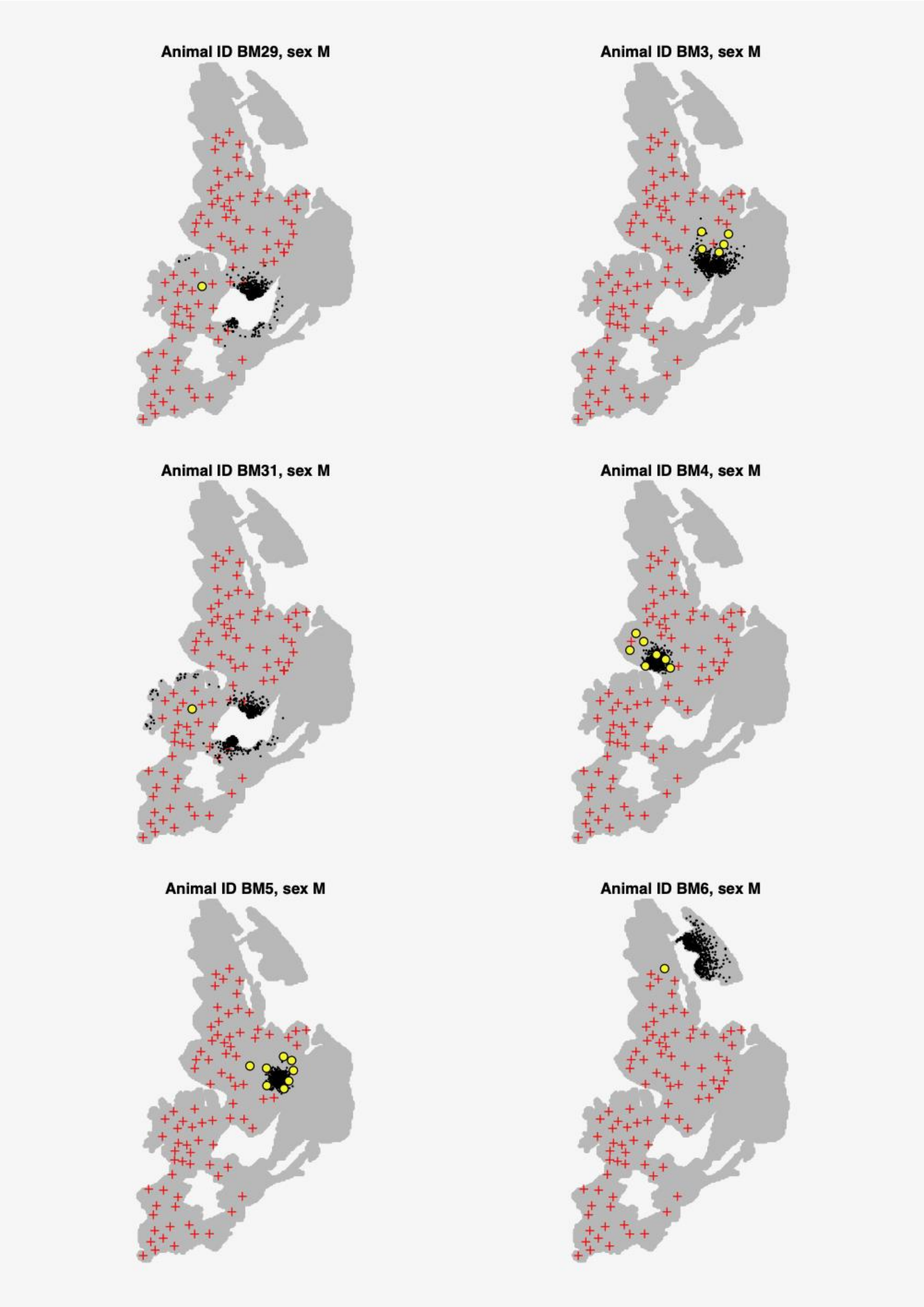
Animal ID BM23, sex M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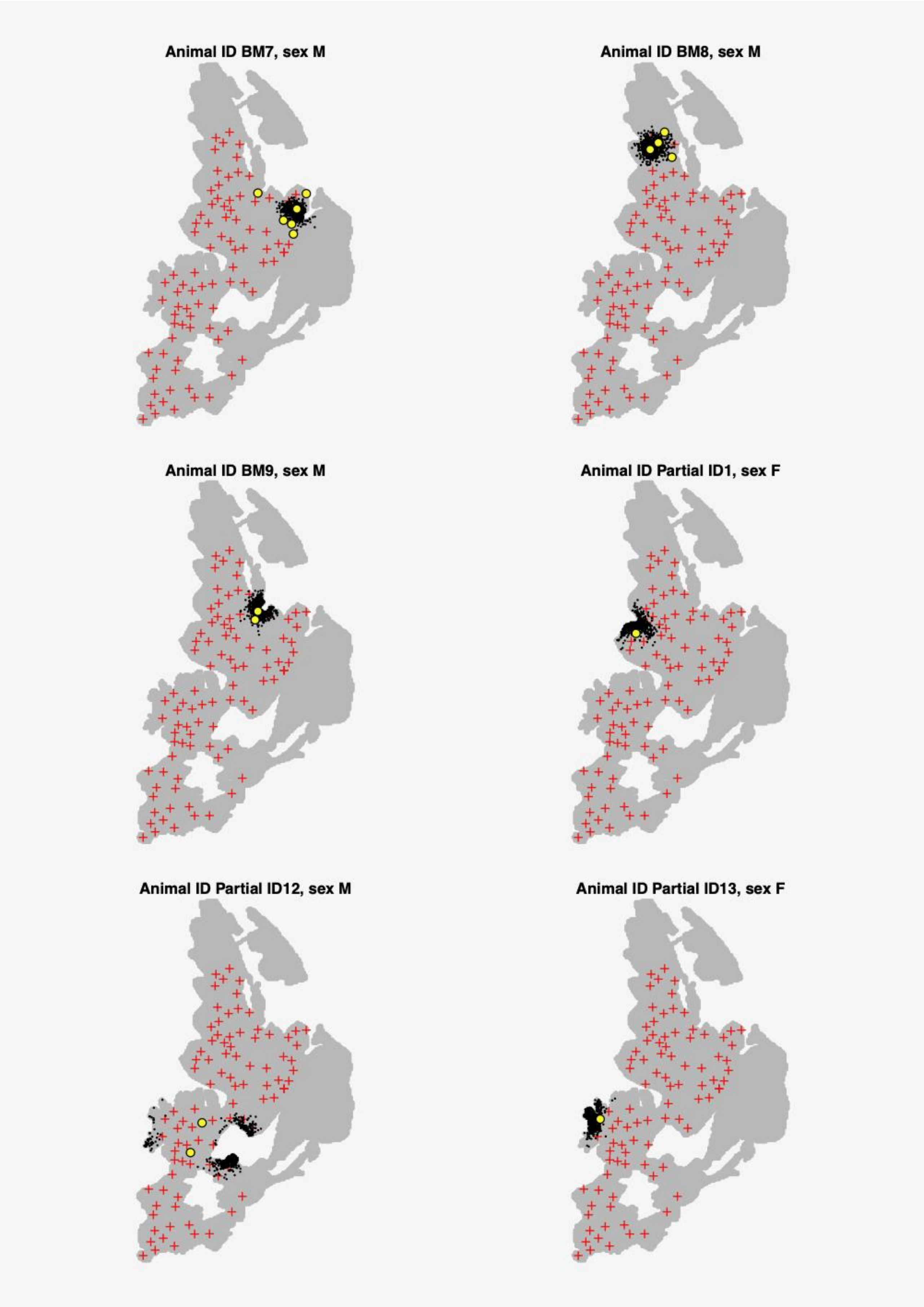

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Animal ID BM9, sex M
Animal ID Partial ID1, sex F
Animal ID Partial ID12, sex M
Animal ID Partial ID13, sex F

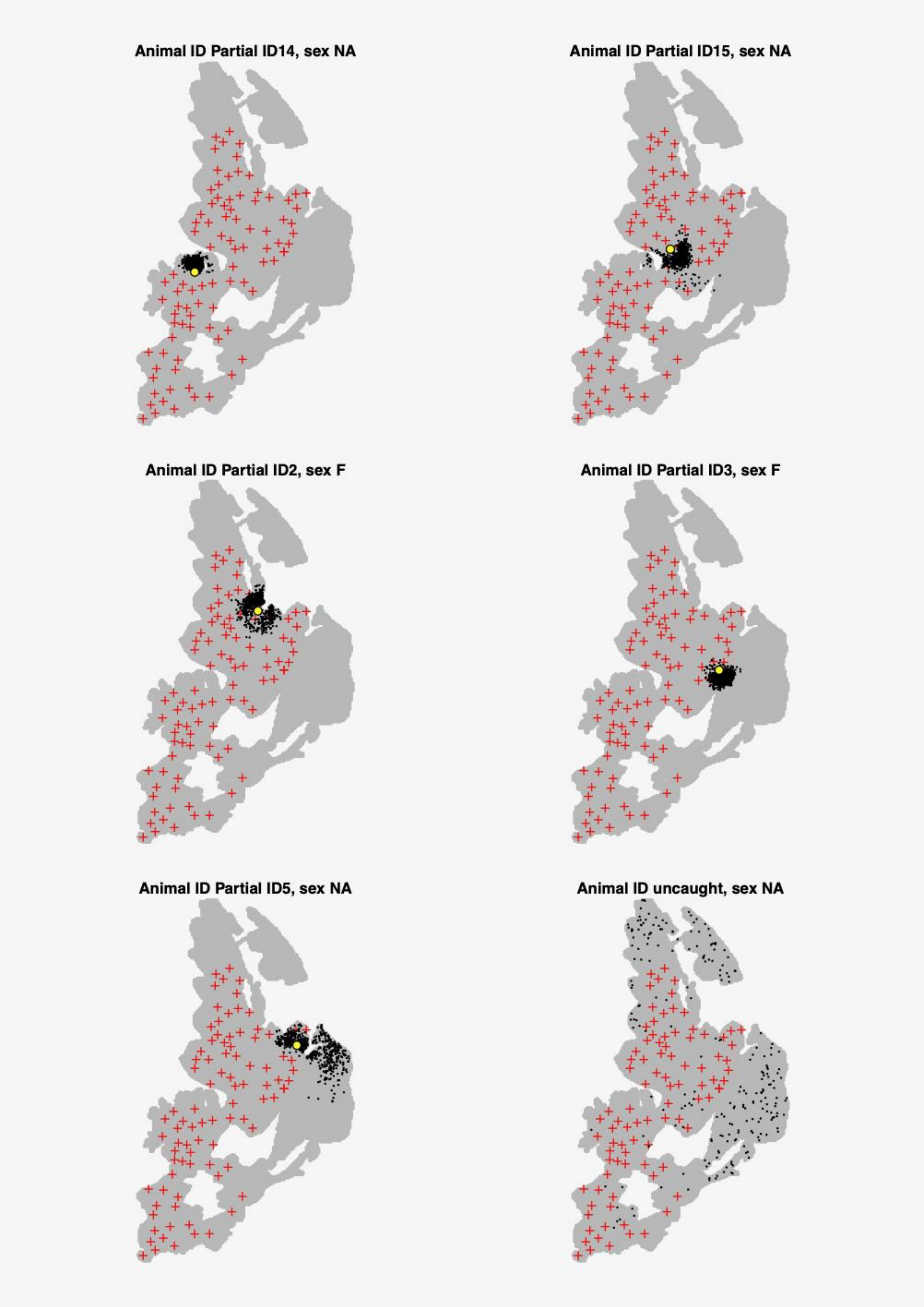
Animal ID Partial ID14, sex NA
Animal ID Partial ID15, sex NA
Animal ID Partial ID2, sex F
Animal ID Partial ID3, sex F
Animal ID Partial ID5, sex NA
Animal ID uncaught, sex NA

Figure S2. Individual leopard activity centre posterior distributions. Activity centre posterior distributions (black dots); capture locations (yellow circles); and trap locations (red crosses) for adult female and adult male leopards in the Boland Mountain Complex, Western Cape.