Evidence for a critical leopard conservation stronghold from a large protected landscape on the island of Sri Lanka

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ARTICLE INFO

ABSTRACT

The decline and extirpation of large carnivore populations can lead to cascading effects in natural ecosystems. An understanding of large carnivore population densities, distribution and dynamics is therefore critical for developing effective conservation strategies across landscapes. This is particularly important in island environments where species face increased extinction risk due to genetic isolation coupled with local losses of finite habitat. The Sri Lankan leopard *Panthera pardus kotiya* is one of two remaining island-living leopards on Earth and the only apex predator in Sri Lanka. Despite its iconic status in Sri Lanka, robust research on the species has been limited to only a handful of scientific studies, limiting meaningful scientific recommendations for the species' conservation and management. In this study, we conducted a single season camera trap survey in Sri Lanka's largest protected area, Wilpattu National Park (1317 km^2), located in the country's northwest. Our objective was to estimate key ecological state variables of interest (density, abundance, sex-specific movement and spatial distribution) of this leopard subspecies. Our results indicate that Wilpattu National Park supports a density of 18 individuals/100 km^2 (posterior SD=1.5; 95% HPD interval=16–21) with a mean abundance of 144 (posterior SD=15) individual leopards and a healthy sex ratio (f:m=2.03:1). The estimated activity range for male leopards > 2 years old was 49.53 km^2 (Posterior SD=3.43; HPD interval=43.09–56.41) and for female leopards > 2 years old was 22.04 km^2 (Posterior SD=1.82; HPD interval=18.34–25.65). This density falls at the higher end of published estimates for the species anywhere in its global range, based on similar methods. Given Sri Lanka's limited size, this national park system should be considered as a critical stronghold that maintains a source population of leopards, contributing to the long-term population viability of leopards in the larger landscape.

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1. Introduction

More than 80% of terrestrial vertebrates now have their ranges impacted by intense human pressure (O'Bryan et al., 2020). These pressures are often most exacerbated on islands where invasive species and habitat loss dramatically increase extinction risk due to finite land surface (Blackburn et al., 2004; Sodhi et al., 2009; Spatz et al., 2017; Setiawan et al., 2018). Seminal examples of large felid extinctions on islands include two island populations of tigers *Panthera tigris sondaica* from the islands of Bali and Java, and the extinction of the African leopard *Panthera pardus pardus*, from Zanzibar (Walsh and Goldman, 2007). These extirpations were a result of loss of habitat due to human expansion, the direct killing of tigers and their prey (Dinerstein et al., 2007).

Sri Lanka and its leopard subspecies *Panthera pardus kotiya* Deraniyagala (1956), represents an important model for the challenges of island species conservation in the 21st century. The nation has a dense human population of ~344 persons/km^2 and rapidly expanding infrastructure development that is fragmenting and diminishing the island's remaining forest cover. Until the turn of the 19th century about 80% of Sri Lanka was covered by primary forests (Lindström et al., 2012). The forest cover was reduced to 44% in 1956 and it is now estimated at 29.7% (GOSL, 2000; FAO, 2010; Sri Lanka UN-REDD, 2017; Samarasinghe et al., 2021). Additionally, the country is experiencing significant post-conflict tourism growth (Ranasinghe and Sugandhika, 2018) and wildlife tourism is reliant on national parks and charismatic species such as leopards and elephants (Prakash et al., 2019). Therefore, the conservation of leopards and other terrestrial vertebrates at large requires rigorous science-based monitoring and research.

The Sri Lankan leopard has evolved in an environment devoid of intraguild competition for at least 10,000 y.b.p, or since the end of the last glacial maxima (Miththapala et al., 1996; Manamendra-Arachchi et al., 2005; Wilting et al., 2016). This is important and has potential evolutionary consequences because, except for a handful of the 75 countries where leopards are still extant (Jacobson et al., 2016), they are in competition with higher-order predators such as tigers *Panthera tigris*, lions *Panthera leo*, hyaenids and dholes *Cuon alpinus*. The Sri Lankan leopard represents not only a critical species for the island's ecosystem functionality as a top predator but also for the country's tourism industry. For example, it is the most popular viewing species for visitors travelling to Sri Lankan national parks (Senevirathna and Perera, 2013; Prakash et al., 2019). Despite fulfilling these critical functions, population estimation research on the Sri Lankan leopard has been limited during the past few decades largely owing to the 30-year civil war in Sri Lanka (see Jacobson et al., 2016; Webb et al., 2020; Kittle et al., 2021 and citations within).

Wilpattu National Park (hereafter WNP) is Sri Lanka's largest National Park, and also Asia's second oldest formally declared protected area (declared in 1938). WNP is spatially important for Sri Lankan biodiversity conservation because it is connected to a protected area complex of reserves (ca. 850 km^2), under protection by the Department of Wildlife Conservation (DWC) and the Forest Department (FD). Despite their protected status, unlike WNP, these protected areas have been subjected to anthropogenic pressures and government policies that have facilitated deforestation, encroachment, road development, de-gazettement and downsizing (Gazette 2011/34 2017) (Köpke, 2021). Wilpattu National Park, therefore, represents a potential source population for many wildlife species, including leopards, that could populate the other smaller protected forests in the landscape around it. Given this potential importance, we sought to: (1) estimate the population density and abundance of the Sri Lankan leopard in WNP, (2) estimate sex-specific movements and sex ratio of leopards in WNP, (3) determine spatial hotspots of its population densities (see Gopalaswamy et al., 2012a; Elliot and Gopalaswamy, 2017), (4) contextualize our findings with other similar assessments of leopards across its range
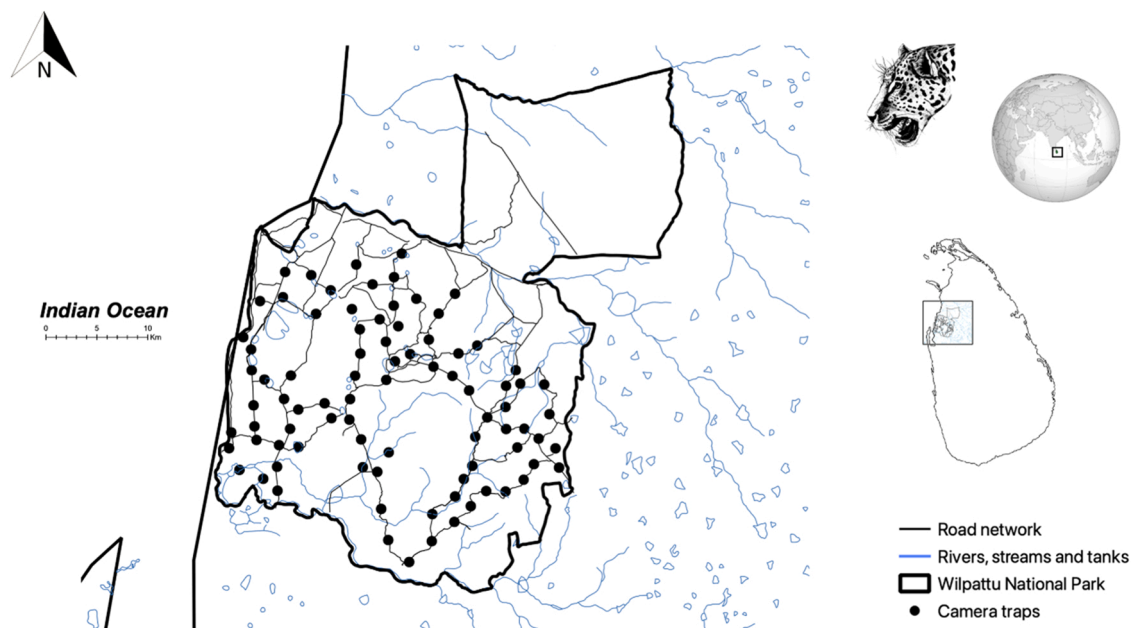

Fig. 1. Map of the Wilpattu National Park (1317 km^2) in Sri Lanka's northwest illustrating our camera trap survey design.

and discuss the potential implications of these results to better inform the management of the WNP protected area complex.

2. Methods

2.1. Study area

WNP (1317 km^2, Fig. 1) is located along Sri Lanka's north-western coast in the country's dry zone. It is bordered by the Indian Ocean on its western boundary, the Kala Oya River in the south, and the Modaragam Aru River in the north. From the north, WNP is connected to Wilpattu North Sanctuary and Mavillu Conservation Forest (2 of 12 connected protected areas in the region). The topography ranges from 0 to 152 m above sea level (average=91 m above sea level (asl) Eisenberg and Lockhart, 1972) and annual temperatures average 27 °C, with two dry periods annually: a short period between January and February, and a longer period from May to September (Mueller-Dombois and Sirisena, 1968; Mueller-Dombois, 1968). Most of the region's rainfall occurs during the first, and second inter-monsoonal periods, between March–April, and September–November (Tomczak and Godfrey, 2003), and averages 1000 mm annually (Eisenberg and Lockhart, 1972). North-Eastern monsoonal rains also occur from December to January (Tomczak and Godfrey, 2003).

The geology of the park can be described by two main groups: the Wanni complex, which is a group of Precambrian metamorphic rock found in the eastern areas of the park, and the Miocene limestone, located in the west (Katz, 1975). This geology gives rise to a diverse array of landform features, which includes beach, dunes, sea cliffs and limestone ridges (Eisenberg and Lockhart, 1972). The coastal landforms transition into large Miocene limestone-karst plains further inland, with scattered circular dolines (locally known as Villus or Wila) that form seasonal lakes, shallow pans and ponds with sandy shores and are ephemeral water sources for wildlife (Eisenberg and Lockhart, 1972). The inland landforms also represent Gneiss-Granite flat plains, with rocky knobs and inselbergs, incised with streams (Eisenberg and Lockhart, 1972).

The park's vegetation belongs to three main categories: littoral vegetation with salt grass and low scrub immediately adjacent to the beach; low stature monsoon scrublands transitioning into monsoonal forests with tall emergent trees such as Indian ironwood *Manilkara hexandra*, Ceylon satinwood *Chloroxylon swietenia*, Peacock chaste tree *Vitex altissima*, Weera *Drypetes sepiaria* and Ceylon ebony *Diospyros ebenum* that form the main forest type in the park (Eisenberg and Lockhart, 1972). Other mid-sized and large mammals in the park that would require large spatial areas to maintain their ecology and behaviours include the Sri Lankan sloth bear *Melursus ursinus inornatus*, Sri Lankan elephant *Elephas maximus maximus*, spotted deer *Axis axis*, sambar deer *Rusa unicolor*, barking deer *Muntiacus muntjak malabaricus*, jungle cat *Felis chaus*, and golden jackal *Canis aureus naria*.

2.2. Field methods

We implemented a single-season camera-trap survey (sensu Karanth and Nichols, 1998) in WNP between 6th May – 16th September 2018. The survey was conducted during the dry season in two plots over two consecutive sessions. Plot 1, in the eastern section of the park was surveyed between 06th May–18th June 2018 (46 days; 1630 trap nights). Plot 2 was surveyed in the western part between 29th July–16th September 2018 (47 days; 1776 trap nights; Fig. 1). We used CuddebackTM 20-megapixel colour X-change camera traps during our survey and set these in a paired format across 40 locations in Plot 1, and 45 locations in Plot 2 (Fig. 1). We set camera traps along game trails, dry stream beds, and motorable park roads as leopards are known to regularly travel, hunt and scent mark along them (Bailey, 1993; Stander, 1998; Balme et al., 2009). We identified prospective locations using a Google Earth satellite map and initially marked 45–70 candidate sites in each plot and then selected the most suitable sites by exploring these locations on foot (du Preez et al., 2014). We noted all evidence of potential leopard presence including droppings, scrapes and tracks during the foot surveys, and used this information to select our final sample locations from the list of candidate sites.

The final trap polygon area covered by camera stations in both plots covered ~660 km^2. Each camera trap site consisted of two camera traps, which were fixed to a tree or wooden stake, and positioned perpendicular to the trail, road, or stream bed, facing each other. Depending on the terrain, we maintained 1.5–2.0 m between the camera trap and the edge of these pathways to cover a wide-angle image (approximately 50 degrees) for each detection. Wherever possible, cameras were placed in a North-South orientation to avoid the glare caused by the sun during sunrise and sunset. Piles of branches and leaves were placed to the left, right and behind each camera trap extending at least 1.5 m to minimize leopards from straying off the pathways, as leopards are known to move around and avoid even the smallest obstacle across their path (DJSS pers. obs.). We also optimized the height of camera traps (30–40 cm from the ground) to capture high-quality images of leopards for identification.

We spaced our camera traps based on other authors' recommendations, which used the radius of the smallest theoretical leopard female home range area (8.7 km^2 - Seidensticker et al., 1990; 16 km^2 - Odden and Wegge, 2005; 23 km^2- Fattebert et al., 2016) to space camera trap stations (e.g., du Preez et al., 2014; Braczkowski et al., 2016), to ensure that at least one detector is placed within a home range area of every animal available in the landscape. The resultant mean trap spacing in our study was 1.93 km. Each camera trap station was checked every 4–6 days to correct camera positioning from animal damage and replace memory cards and batteries. Most camera trap stations were accessible by jeep and on foot, except for one location that was only accessible by boat. Camera traps were set to burst mode, taking five images every time, the thermal-motion sensor was triggered, followed by a 20 or 30 s video. All images were classified to the species level (to account for non-leopard images) and for leopards to the individual level.

Individual leopards were identified from the unique rosette and spot patterns on their pelage (Pereira et al., 2022). Adult leopards also have some of the most pronounced sexual dimorphism in the family Felidae (Balme et al., 2012). We were therefore able to classify the sex of individuals by using distinctive morphological characteristics such as the presence of testes, an enlarged dewlap, and a
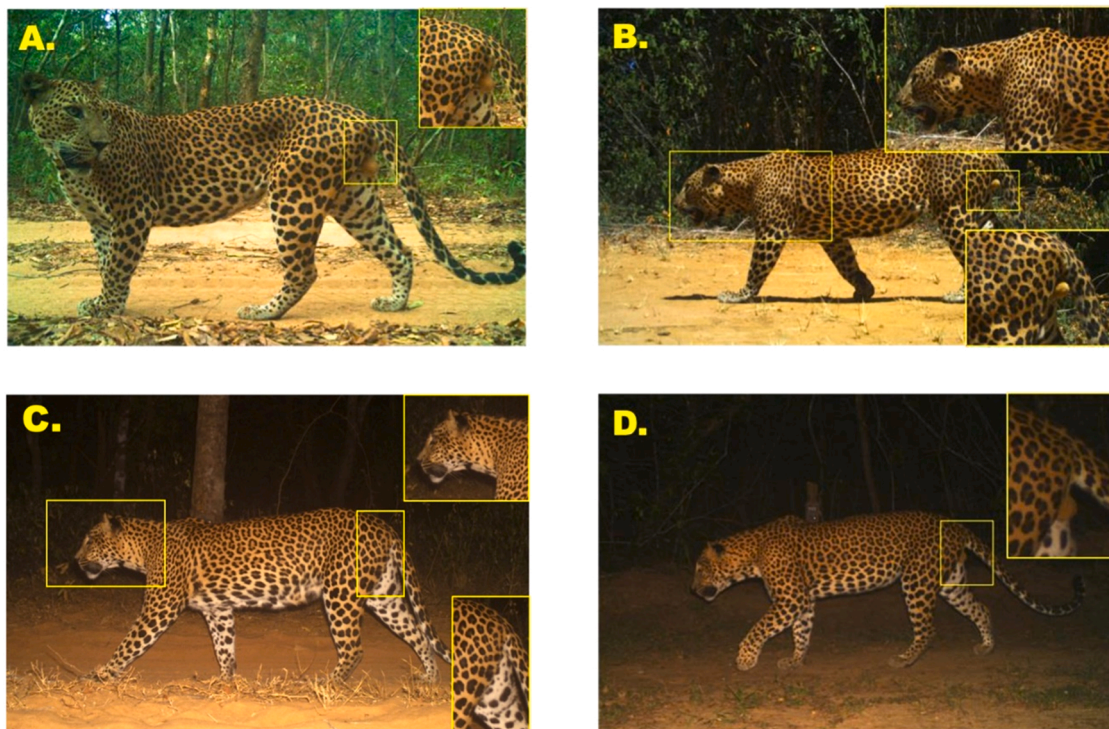
Fig. 2. We followed Balme et al. (2012) to identify and sex the leopards in WNP. Photograph A shows adult male leopard 22 (camera trap station 80) with prominent testes; photograph B shows adult male leopard 33 (station 48) with large dewlap, prominent sagittal crest and testes; photograph C shows adult female 91 (station 68) with slender head and no testes; while photograph D shows young adult male 11 (station 4) identified through the presence of a dewlap and testes.

sagittal crest in adult males (Balme et al., 2012; Fig. 2). The first, seventh and eighth authors independently assigned individual identities to temporally unique photographs, and we included individuals only where there was consensus amongst the assessors (Alexander et al., 2015; Bahaa-el-din et al., 2015). We excluded a total of eight images of poor quality. Dependent cubs (typically <2 years) were excluded from all analyses due to their non-independent capture probabilities and low survival rate (Karanth and Nichols, 1998; Balme et al., 2019). These unique leopard identities were then used to produce individual capture histories. For this purpose, we defined 24-hr sampling occasions, such that we considered only one capture per individual leopard per station per calendar day (Balme et al., 2019). Multiple captures of the same individual at the same location on a single sampling occasion were discarded.

2.3. Analytical framework

We estimated leopard population density in WNP using spatially explicit capture-recapture (SECR) analyses. For this, we utilized both a maximum likelihood (Borchers and Efford, 2008) and Bayesian framework (Royle et al., 2009). We used the former as it has been the most widely used inference method of SECR analysis for leopards throughout its range (Table S2). We also opted to use the Bayesian approach as it is considered a more robust option since it does not rely on asymptotic arguments and are valid irrespective of sample size (Royle et al., 2009). Furthermore, a crucial parameter of interest among large mammal researchers and conservationists is the sex ratio (e.g., Elliot and Gopalaswamy, 2017). However, these two modelling approaches handle the estimation of this parameter differently, especially when there are individuals in the dataset who can be uniquely identified but cannot be assigned to a specific sex – a ubiquitous problem in camera trap studies (Efford, 2020; Laguardia et al., 2021). Hence, in this study, we also compare estimates of sex ratio using the two methods.

For this exercise, we developed a habitat mask and a state space, for the maximum likelihood and Bayesian frameworks, respectively. Considering the available habitat extent beyond WNP, and the fact that a smaller buffer is likely to produce unreliable density estimates (Chase Grey et al., 2013; Braczkowski et al., 2016), we created a buffer extending 30 km beyond the extremes of our camera trap array to ensure that all activity centres of individuals potentially exposed to sampling were included but animals centred in the edge of the buffer has a negligible chance of being detected (Efford, 2019). We generated a habitat mask /state space across our study area and the extended buffer area (2195 km^2) in the form of 0.3364 km^2 (i.e., 0.580 km x 0.580 km, Gopalaswamy et al., 2012a) equally-spaced pixels. We created this in Quantum GIS (QGIS Development Team, 2019). We excluded pixels within areas of non-leopard habitat: mainly ocean, water bodies and densely populated towns, as leopards are unlikely to have their activity centres in these locations (Royle et al., 2009). We also included a measure of camera trap effort through a binary matrix of active-inactive days

Table 1
Model description.

Model type		Model description
Model 1	$(g_0/\lambda_0)\sim 1$, σ ~ 1	based on the assumption that both basal detection probability/rate and the rate of decline in detection probability/rate is independent of sex
Model 2	$(g_0/\lambda_0)\sim 1$, σ $\sim$ sex	based on the assumption that rate of decline in detection probability/rate is sex-specific but basal detection probability/rate is independent of sex
Model 3	$(g_0/\lambda_0)\sim$ sex, σ ~ 1	based on the assumption that the rate of decline in detection probability/rate is independent of sex but the basal detection probability/rate is sex specific.
Model 4	$(g_0/\lambda_0)\sim$ sex, σ $\sim$ sex	based on the assumption that rate of decline in detection probability/rate and basal detection probability/rate are sex specific.

(camera active=1 and camera not active=0) for each camera station. Camera stations were considered active if at least one camera trap was functioning during that occasion.

Sex covariates are known to influence the observation process, especially among big cats (Sollmann et al., 2011). To factor this into our analysis, we included sex-specific covariates to describe the basal detection probability/rate (g_0/λ_0) and the scale parameter (σ), which is related to movement. In total, we confronted four candidate models in our analyses (Table 1).

We used the package "secr" version 4.3.1 (Efford, 2020) in R 4.0.2 (R Development Core Team (2020)) to obtain density estimates using a maximum likelihood approach. The recommended option in the package secr (Efford, 2020) to estimate sex ratio when some individuals cannot be assigned to a sex category is the hybrid mixture (*hcov*) approach. Therefore, we were able to include eight independent unsexed individuals (>2 years) into the analysis. Models were run using the full likelihood option for proximity detectors. Models were selected using an information-theoretic approach, with the Akaike information criterion corrected for a small sample size (AICc; Burnham et al., 2011). The most parsimonious; model based on parameters was selected based on the highest ranked model by AIC.

We used a modified version of SCRBayes (https://github.com/jaroyle/SCRbayes) within the programming environment R (Version 3.6.1; R Development Core Team 2019) to analyze the Bayesian version of the models by applying Bayesian Markov Chain Monte Carlo (MCMC) methods (Tierney, 1994; Elliot and Gopalaswamy, 2017; Braczkowski et al., 2020). We set four chains to run each model with each chain defined to be 100,000 iterations. We discarded some initial iterations, and on occasion a chain, if MCMC convergence was problematic. In order to assess MCMC convergence for all models, we used the Gelman– Rubin statistic, R-hat, with a value of below 1.1 indicating convergence (Gelman and Hill, 2006). In addition to the Gelman–Rubin statistic, we also used the Geweke diagnostic for each chain to assess convergence (z-score<|1.64| implies convergence) to improve model selection accuracy.

We used the Bayesian p-value based on individual encounters (Royle et al., 2009) to assess model adequacy. We utilized the Harmonic Mean estimator of the Marginal Likelihood (MLHM; Dey et al., 2019a), along with visual inspection of pairwise correlation plots between parameters from the posterior MCMC draws, to infer on model choice (Dey et al., 2019a; Elliot and Gopalaswamy, 2017; Broekhuis et al., 2021; Braczkowski et al., 2020). Visual inspection assisted us in assessing if the abundance parameter was, in particular, correlated with any other parameter.

In addition, we also calculated activity range size based on σ using the bivariate normal kernel estimator following (Broekhuis et al., 2021) and Braczkowski et al. (2020). We explicitly use the term 'activity range' instead of 'home range' to recognize that this range is restricted in time to the period of camera trap sampling.

In order to calculate abundance in the effectively sampled area around our camera trap array, we defined a buffer using the recommendation provided in Royle et al. (2014)). We created a buffer using the weighted average of the posterior mean estimates of sigma, weighted by the sex ratio. Accordingly, a buffer width corresponding to square root of the value obtained from the chi-squared distribution table at an alpha level of 0.05 and 2 degrees of freedom was used. This width corresponds to 95% of the leopard movement outcomes during this study.

Furthermore, to determine spatial hotspots of leopard densities across the study area, we generated a heat map to show variations of posterior densities of leopards for each potential home range centre (pixels) across the state space using the Bayesian analytical framework (Gopalaswamy et al., 2012a). We do note that the pixelated density hotspots are restricted to area sampled in the vicinity of the camera trap array.

3. Results

3.1. Leopard detections and observed population structure

The total sampling effort of the survey was 3406 trap nights. Only 4 (5%) of the 85 trap locations did not record leopards during the survey period. From the sample of leopard detections, we successfully identified 133 individual leopards. We identified 116 of these to be independent leopards (i.e., >2 years), and could positively ascribe sex to 108 of these, resulting in 45 males (42%) and 63 females (58%). From the 116 leopards, a total of 552 temporally independent leopard detections (265 male detections, 277 female detections and 10 detections of unknown sex) were recorded. Eight adult females were observed with 1–2 dependent cubs (age < 2 years, total n = 17 cubs) (Table S1). Detection rates of individual leopards ranged from 1 to 23 (mean = 5) during the sampling period.

Table 2

Model rankings under the Bayesian framework based on visual inspection of the correlation between σ vs. λ_0 from the correlation plots for each model (Fig. S1).

Rank	Model No.	Model parameters	Marginal Likelihood using HM method
1	Model 2	λ_0~1, σ~sex	-530282.5
2	Model 4	λ_0~sex, σ~sex	-533172.5
3	Model 3	λ_0~sex, σ~1	-519906.4
4	Model 1	λ_0~1, σ~1	-518914.4

Table 3

Spatial capture-recapture models fitted using hybrid mixture models (hcov) in the maximum likelihood framework. Models were ranked according to their Akaike weights (w_i) based on the Akaike Information Criterion for small samples (AICc).

Rank	Model No.	Model	Ka	Log likelihood	AICc	ΔAICc	wi
1	Model 2	g_0~1, σ~h2	5	-871.428	1753.402	0	0.63
2	Model 4	g_0~h2, σ~h2	6	-870.858	1754.487	1.085	0.37
3	Model 3	g_0~h2, σ~1	5	-898.79	1808.126	54.724	0
4	Model 1	g_0~1, σ~1	4	-911.907	1832.174	78.772	0

Table 4

Parameter estimates from the Bayesian SECR analysis, during from May-September 2018 in Wilpattu National Park [Posterior mean (Posterior SD), (95% highest posterior density interval)]. Here, ψ is the proportion of the data augmented individuals, which are real. And ψ_{sex} is the proportion of the population which are females.

Bayesian analysis	σ (km)		λ_0	ψ	ψ_{sex}	Posterior Mean Density (Posterior SD) Individual leopards $<$ 2 years per 100 km^2
	M	F				
Model 1	1.42(0.04)	1.42(0.04)	0.094(0.007)	0.417(0.036)	0.582(0.053)	15.49(1.18)
	(1.34–1.50)	(1.34–1.50)	(0.081–0.108)	(0.348–0.489)	(0.477–0.684)	(13.21–17.82)
Model 2	1.62(0.06)	1.08(0.05)	0.106(0.008)	0.495(0.044)	0.670(0.046)	18.41(1.50)
	(1.52–1.73)	(0.99–1.17)	(0.090–0.123)	(0.408–0.577)	(0.578–0.759)	(15.67–21.55)
Model 3	1.40(0.04)	1.40(0.04)	0.133(0.013)	0.434(0.038)	0.616(0.051)	16.14(1.25)
	(1.32–1.47)	(1.32–1.47)	(0110–0.159)	(0.359–0.505)	(0.518–0.714)	(13.76–18.59)
Model 4	1.65(0.06)	1.65(0.06)	0.099(0.010)	0.500(0.046)	0.671(0.047)	18.61(1.58)
	(1.53–1.47)	(0.92–1.15)	(0.080–0.120)	(0.414–0.593)	(0.575–0.757)	(15.49–21.64)

3.2. Bayesian MCMC diagnostics

We expected and found that it was necessary to ensure that both the Gelman-Rubin (for multiple chains) and the Geweke diagnostic for each chain were used to achieve adequate levels of convergence (r-hat $<$1.1 and |z-score|$<$1.64) to achieve stability in the MLHM values for each model. To achieve convergence with these criteria, we used 90,000 MCMC draws and 3 chains for Model 1, 91,000 draws and 2 chains for Model 2, 32,000 draws and 3 chains for Model 3 and 60,000 draws and 4 chains for Model 4.

3.3. Model adequacy and model choice

We obtained a Bayesian p-value of $>$ 0.90 for all four models indicating model inadequacy (Royle et al., 2009). We did not use other measures of Bayesian p-value (for example, Gopalaswamy et al., 2012b utilize a Bayesian p-value measure involving total encounters).

We assessed the pairwise correlation plots (Elliot and Gopalaswamy, 2017; Elliot et al., 2020; Braczkowski et al., 2020) for assessing parameter identifiability and as an important consideration for model selection. Based on these plots, Models 2 and 4 indicated the least parameter identifiability issues among the sex-specific models (Fig. S1). This assessment yielded a model selection ranking similar to the one based on AICc for the maximum likelihood models (Tables 3 & 4).

In addition, we carried out model selection using the natural logarithm of the marginal likelihood using the HM estimator (MLHM) from Dey et al. (2019a). This method indicated that the null model (Model 1) (Table 1), produced the highest log likelihood estimate (log likelihood = −518,914.4, Table 2), differing from our inferences from the correlation plots and the AIC assessments of the equivalent maximum likelihood models (Table 3). We also note that for the maximum likelihood models, only Models 2 and Model 4 received significant model weights. Therefore, we used the MLHM values to only assess if models produced values which were significantly different (a few orders different). Since this was not the case, we used inference from correlation plots as the more important factor to rank our models.

Table 5

Parameter estimates from the maximum likelihood framework employing secr, during from May-September 2018 in Wilpattu National Park. [Parameter estimate (SE), (95% confidence interval)]. Here, Pmix is the mixture parameter yielding ratios, which are assumed to be sex ratios.

Maximum likelihood analysis	σ (km)		g_0		Pmix		Density (SE) (Individual leopards <2 years per 100 km^2)
	M	F	M	F	M	F	
Model 1	1.42(0.04) (1.35–1.50)	1.42(0.04) (1.35–1.50)	0.091(0.006) (0.089–0.117)	0.091(0.006) (0.089–0.117)	0.417(0.047) (0.327–0.512)	0.583(0.047) (0.489–0.672)	15.35(1.44) (12.78–18.45)
Model 2	1.64(0.06) (1.53–1.75)	1.11(0.04) (1.04–1.19)	0.102(0.007) (0.089–0.117)	0.102(0.007) (0.089–0.117)	0.403(0.047) (0.316–0.497)	0.597(0.047) (0.503–0.684)	16.19(1.53) (13.46–19.47)
Model 3	1.41(0.04) (1.34–1.49)	1.41(0.04) (1.34–1.49)	0.127(0.012) (0.105–0.152)	0.072(0.006) (0.061–0.085)	0.402(0.047) (0.315–0.496)	0.598(0.047) (0.504–0.685)	15.52(1.46) (12.91–18.65)
Model 4	1.67(0.06) (1.55–1.80)	1.09(0.04) (1.01–1.18)	0.095(0.010) (0.077–0.115)	0.111(0.012) (0.090–0.136)	0.405(0.047) (0.317–0.500)	0.595(0.047) (0.500–0.682)	16.19(1.53) (13.46–19.47)

3.4. Density estimates

As expected, under both analytical methods the null model (Model 1) produced nearly identical estimates of the important ecological parameters (in our case, density and sex ratio) since no information about sex effects are incorporated in the model and the estimated sex ratios are only the observed sex ratios (Tables 4 and 5). The posterior mean estimates for the Bayesian models differed only slightly from the likelihood-based estimates and were more pronounced for the top two models (Models 2 and 4) (Table 4).

Based on the Bayesian framework, the posterior mean leopard density within our study area based on model 2 was 18.41 (posterior SD=1.50; 95% highest posterior density (HPD) interval= 15.67–21.55) individuals > 2 years old/100 km^2. The rate of detection reduced rapidly away from the activity centre (σ) at 1.08 km (posterior SD=0.05) for females and 1.62 km (posterior SD=0.06) for males (Table 4). We reported detection probability (g0) of 0.106 (posterior SD=0.008).

The posterior mean abundance for the total buffered area (Nsuper) was estimated at 404.13 (posterior SD= 33.03; 95% HPD interval=338.00–467.00) leopards > 2 years old. More importantly, the measured posterior mean abundance within the effectively sampled area was 143.75 (posterior SD = 14.60) leopards > 2 years old. Posterior density estimates for each 0.3364 km^2 pixel indicate "density hotspots" spread throughout the central and western sections of the study area (Fig. 3).

The maximum likelihood framework (using secr) yielded a slightly lower estimate, Models 2 and 4 were the top-ranking models (<2 ΔAICc) (Table 3). However, the log-likelihood values differ by about 1.4 units. And the 95% confidence interval of the extra-parameter corresponding to Model 4 did not overlap with zero, indicating that this parameter indeed contributed in some way to model identity (Leroux, 2019). The leopard density from our top-ranking model for WNP and the accompanying habitat mask was estimated at 16.19 (SE=1.53; 95% Confidence Interval (CI)= 13.46–19.47) individuals > 2 years old/100 km^2 (Table 5). The rate of detection reduced rapidly away from the activity centre (σ) at 1.11 km (SE=0.04) for females and 1.64 km (SE=0.06) for males (Table 5). There was no difference in detection probability (g0) of both males and females, and the model yielded a probability of 0.102 (SE=0.007) for both sexes. The abundance of the entire buffered area of 2195 km^2 (expected N) was 355 (SE=34, 95% CI=295–427) individual leopards > 2 years old.

3.5. Activity range and sex ratios

Activity range was estimated based on the sigma value of our top model in the Bayesian framework, using the bivariate normal kernel estimator. The estimated activity range for male leopards > 2 years old was 49.53 km^2 (Posterior SD=3.43; HPD interval=43.09–56.41) and for female leopards > 2 years old was 22.04 km^2 (Posterior SD=1.82; HPD interval=18.34–25.65).

Based on our best model from the Bayesian analysis as estimated by ψ_{sex}, we estimated there to be 1 male: 2.03 female leopards (Table 6) for the top model (Model 2). However, using the Pmix value in the likelihood framework, we obtain an indicative sex ratio of 1:1.48 for the equivalent top model (Table 6). This is very similar to the observed sex ratio of the study, which was 1 male:1.40 females. Clearly, in our study, the choice of analytical approach made a difference with regards to sex ratio estimation.

4. Discussion

In this study, we sampled a large, heterogenous area, in order to better represent the population density of leopards on WNP, Sri Lanka's largest national park. Here, we build up on an earlier study to fill an important gap in the population density estimation literature of one of the most understudied leopard subspecies, and the second remaining island leopard population (Kittle et al., 2021; Table S2). We found that leopard densities in WNP are amongst the highest reported on Earth in the peer-reviewed literature (Table S2). Additionally, the high number of individuals recorded (116 independent individuals and 17 dependents) and a healthy sex ratio, all recorded during a relatively short study period, is indicative of a healthy breeding population of leopards, and this population should serve as an important source for adjacent protected areas (Dias, 1996).

Leopards occur in low densities in most of their range globally (Table S2), and like most large carnivores are currently declining numerically and geographically (Jacobson et al., 2016). However, high-density, healthy leopard populations are observed in a few
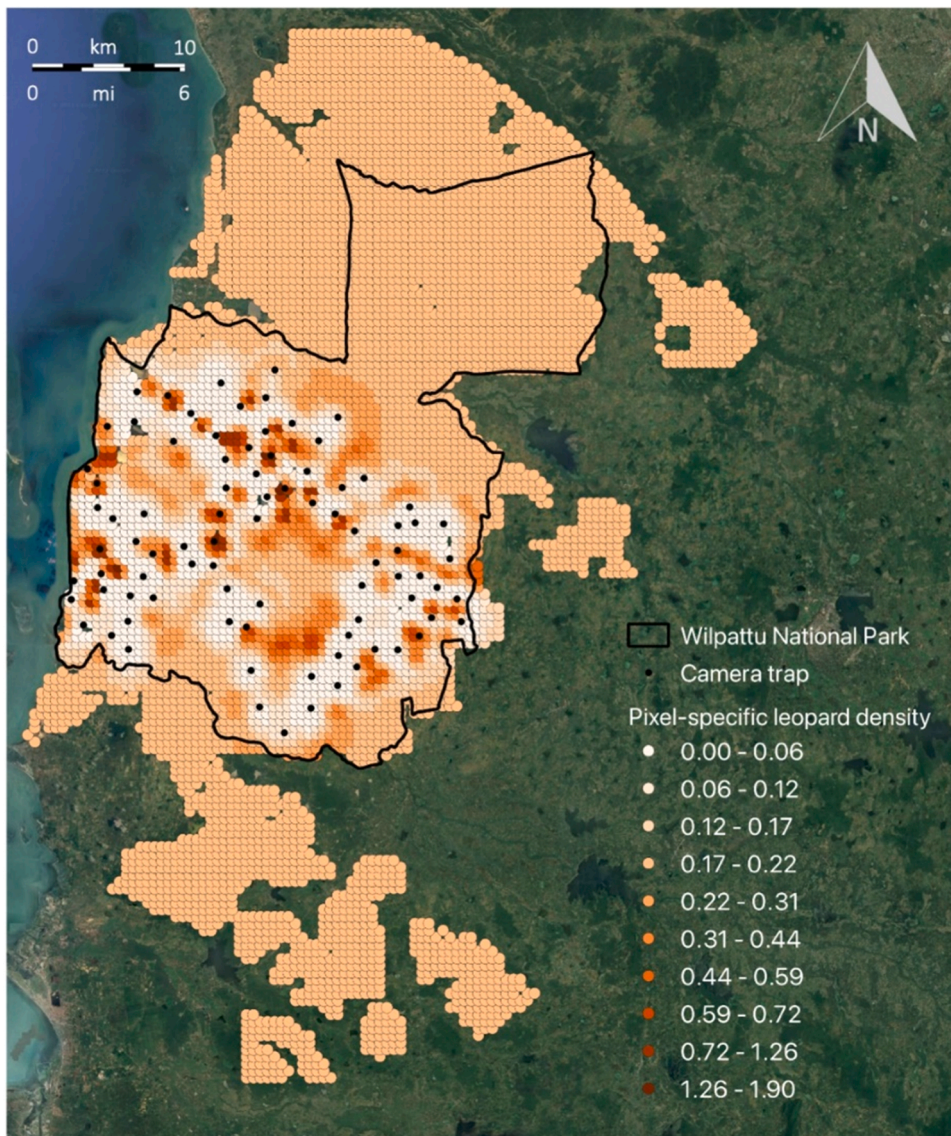
Fig. 3. Bayesian pixel-specific leopard density expressed in units of individual leopard activity centres per state space pixel (0.3364 km^2) across the 30 km state space based on Model 2. Hotspots are found on the central and western sides of the National Park. The areas beyond the camera trap array, but within the state space, is colour-coded with an averaged density (orange). Consequently, these estimates are also accompanied by high uncertainties.

Table 6
Sex ratio of leopards recorded in the Wilpattu camera trap survey in 2018.

Model number	Sex ratio (Female:Male)	
	Bayesian	Maximum likelihood
Model 1	1.40	1.40
Model 2	2.03	1.48
Model 3	1.60	1.49
Model 4	2.04	1.47

prey-rich, often well-protected landscapes in Sri Lanka, India, Java, Indonesia, South Africa and also some fenced landscapes in the African continent (Table S2). In comparison with these populations, the Sri Lankan population is unique, since the leopard has been the only big cat and apex predator on the island for at least 10,000 years (Manamendra-Arachchi et al., 2005). Moreover, presently, almost 50% of the Sri Lankan leopard's range falls within protected areas that are largely free from direct human persecution and poaching of

preferred prey (Jacobson et al., 2016; Kittle et al., 2018). Against this backdrop, it can be hypothesized that there could be differences in behavioural and social characteristics unique to the Sri Lankan leopard. For example, there are two components associated with the parameter basal detection rate/probability (see Dey et al., 2019b): (1) a component that describes the frequency with which leopards visit the detectors (an ecological process) and (2) a component that describes detector efficiency (an observation process). The parameters g_0/λ_0 do not distinguish between these two components. If we assume that the second component is constant among sites, we notice that studies conducted in Sri Lanka yield the highest estimates of g_0/λ_0, thereby indicating a unique behavioural characteristic–an unusually high usage of the road network in typical reserves (see Tables S3). The absence of any interspecific carnivore competition, together with an abundance of prey could be major reasons. We caution, however, that these interpretations of g_0/λ_0 could be conflated with the issue of compensatory heterogeneity, where sex-based and other differences in activity range size could potentially cause heterogeneity in basal detection rates (Efford and Mowat, 2014). Hence, upon factoring this, it would be interesting to assess these basal detection parameters in other similar landscapes across the leopards' range that are free from anthropogenic mortalities and interspecific competition.

The population of leopards in WNP has a high prevalence of females: a 1:2 male:female ratio, within a population density of 18 leopards > 2 years/100 km^2, which is consistent with previous leopard studies (Bailey, 1993; Mizutani and Jewell, 1998; Webb et al., 2020) and also similar to other top predators such as tigers (Smith and McDougal, 1991) or lions (Elliot and Gopalaswamy, 2017) in prey-rich source populations. Our study also highlights the importance of using the most appropriate analytical approach, in our case SECR models conditioned on N (Royle et al., 2013, 2015; Dey et al., 2019a & b) to accurately estimate sex ratios. As noted in the package secr manual (Efford, 2020), given that the likelihood is conditioned on density, it may not be possible to interpret the estimate of the mixture parameter from the *hcov* model strictly as sex ratio (Laguardia et al., 2021). This nuance appears to have gone unnoticed in practice. For example, India's official, country-wide, large felid status assessments of leopards (Jhala et al., 2021) and tigers (Jhala et al., 2015; Jhala et al., 2020), and even a local status assessment of lions (Gogoi et al., 2020), appear to assume that the mixture parameter reveals true sex ratios. Other studies (e.g., Kumar et al., 2019 and Kittle et al., 2021) have also made this assumption.

Female leopards require access to high-quality habitats to raise cubs and their home ranges are based on the spatio-temporal changes in prey distribution (Bailey, 1993; Odden and Wegge, 2005). Female leopards also have smaller home ranges while males tend to range more widely to increase access to females (Owen, 2013; Snider et al., 2021). Similar patterns are observed among other solitary carnivores (Macdonald, 1983). Our results also show these observed trends in male and female activity range sizes which provides an indication of an approximate home range size (see Section 3.5 in results). These are also quite similar to home range sizes observed in India (Odden and Wegge, 2005; Snider et al., 2021). With the high number of females and cubs (Table S1) recorded in our study, our results are clearly indicative of the presence of a healthy prey base inside the park. In total, we recorded 17 dependent cubs (< 2 years old) during the course of the study period. This suggests that there may be a healthy recruitment cohort within the WNP population. However, further long-term studies are required to quantify actual recruitment into the adult population.

Leopards, like many solitary polygynous mammals, generally exhibit female philopatry and male-biased natal dispersal (Balme et al., 2017; Fattebert et al., 2015, 2016; Greenwood, 1980; Naude et al., 2020). Populations could be regulated by density-dependent controls such as infanticide, social strife and territoriality that regulates population growth in carnivores (Cariappa et al., 2011; Kissui and Packer, 2004). Therefore, space and density-dependent regulatory mechanisms also play a role in population regulation rather than only prey (Cubaynes et al., 2014; Wallach et al., 2015). Many mammals disperse from their natal range and establish new territories to avoid such competition for space and resources and avoid inbreeding (Greenwood, 1980; Liberg and von Schantz, 1985). It is therefore important to have secure core areas with ecological connectivity in the surrounding landscape to allow dispersal and its associated behavioural, ecological, and genetic processes to persist, and sustain healthy populations.

Inbreeding depressions can lead to reduced fitness and make individuals in a population vulnerable to diseases and other risks (Charlesworth and Willis, 2009). In our study, we observed a total of nine individuals with distinctly kinked tails, resembling those reported in inbred populations of *Puma concolor* from Florida (Florida panther) (O'Brien, 1990; Wilkins, 1997) and California (Ernest et al., 2014) (Fig. S2). Some were kinked near the base of the tail, whereas most were kinked towards the end of the tail (Fig. S2). To ascertain reasons for this, we recommend a study to assess more closely the integrity of this population in the face of potential genetic bottlenecks (Naude et al., 2020) and provision for appropriate conservation strategies (for example, see Wikramanayake et al., 2010; Wikramanayake et al., 2011).

4.1. Strengthening the integrity of the park boundaries and park management

Wilpattu National Park is the largest core area in the landscape with smaller protected area complexes to the north (ca. 407 km^2) and south and southeast (ca. 443 km^2). The density heat map generated via our best-fitting model using the Bayesian approach depicts key "hotspots" within WNP during the study period (Fig. 3). We note, however, that since we have not used specific covariates to model pixel-specific density or abundance, the spatial variation in posterior abundances (Fig. 3) is restricted to the extent supported by the binomial point process model (Royle et al., 2013). Most of the landscape on the eastern boundary of WNP is comprised of agricultural landscapes and a few viable habitats are available with known leopard presence (DJSS per obs.); these agricultural landscapes too could be utilized by leopards, since they are highly adaptable and can reside and breed in such human-dominated landscapes (Kittle et al. 2012; Athreya et al., 2013). However, based on the density heat map generated, relatively lower densities were observed from the southern boundary of the park, suggesting some edge effects in these areas. Even though the southern portion is connected to an adjacent protected areas complex (Fig. 4), we observed several signs of incursions. Local villagers are known to enter the park from the southern boundary and carry out illegal activities inside the park such as wildlife poaching (sambar deer *Rusa unicolor*, spotted deer *Axis axis* and mouse deer *Moschiola meminna* etc.), cut down trees to collect bee honey, and treasure-hunt in archeological sites. Kittle
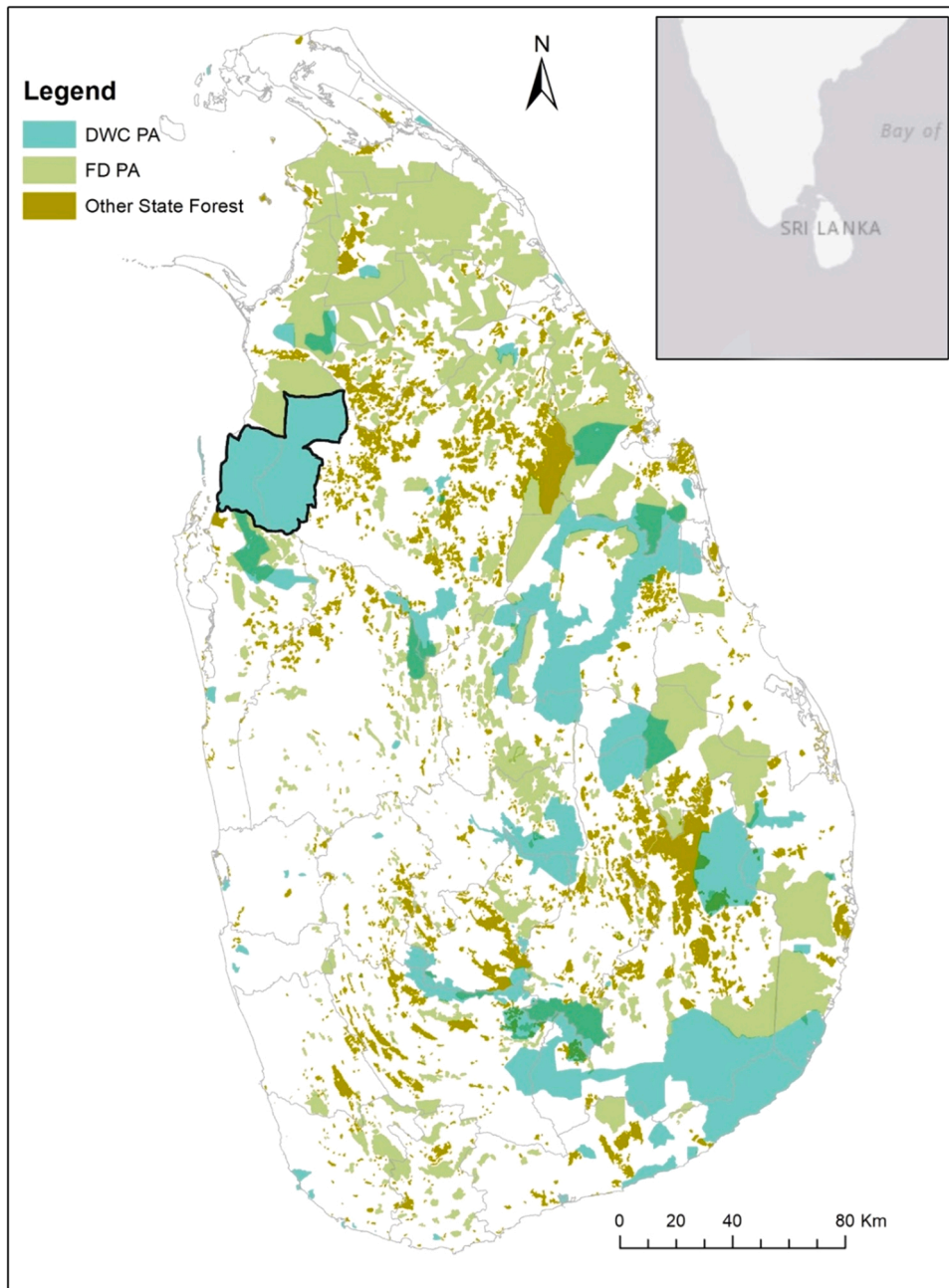
Fig. 4. Forest cover in Sri Lanka (DWC PA, protected area under the Department of Wildlife Conservation; FD PA, protected area under the Department of Forest Conservation; Wilpattu National Park is depicted with a black coloured border).
(Reproduced from Samarasinghe et al., 2021).

et al. (2021) also reports people encroaching into the park for poaching and collecting forest products from nearby human settlements. We observed evidence for several of such incursions inside the park during this survey, and lost camera traps to theft from four stations. It is critical that the DWC effectuate and enforce the provisions of the Flora and Fauna Ordinance 1938 as amended, to mitigate such incursions. The seasonality, impact and intensity of poaching of prey must be investigated and eliminated from the national park as the presence of poaching activity may result in indirect leopard mortalities upon unexpected encounters by poachers and depletion of prey (Henschel et al., 2011). The same ordinance also prescribes limitations and directives for certain development activities within a one-mile radius of any national reserve including national parks. They are vital provisions to ensure PA efficacy (Balme et al., 2010) and strengthen the integrity of the park boundaries.

4.2. Conservation implications: Sri Lanka has an opportunity for effective leopard conservation

This survey demonstrates that WNP supports an important source population of leopards that sustain a larger population in the landscape with satellite protected areas in the north, east and south. Sri Lanka has several such landscapes with high levels of protection that are embedded adjacent to landscapes with lower protection levels, which together form large protected area networks that can be conserved as landscapes with functional ecological connectivity (i.e., Yala National Park). These landscapes, which receive high levels of protection should be considered as core areas that support source populations of leopards in light of robust research (Kittle et al., 2018; Webb et al., 2020). We recommend that the other large national parks should also be surveyed using robust, spatially explicit capture-recapture methods for a better representation of the status of those populations, and inform an island-wide conservation strategy based on rigorous science. We also recommend periodic (bi-annual or annual) surveys of prey species to be carried out within large PAs following rigorous scientific methodologies (e.g., Karanth and Nichols, 2017). This is especially urgent given the recent proposals to release protected forests for development (Samarasinghe et al., 2021), but also to utilize leopard conservation opportunities from Sri Lanka's pledges to international covenants to increase forest cover, such as the Nationally Determined Contributions to the Paris COP and the Bonn Challenge Commitments (Wikramanayake et al., 2020).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02173.

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