

Population dynamics of the last leopard population of eastern Indochina in the context of improved law enforcement[☆]

S. Rostro-García^{a,b,*}, J.F. Kamler^{a,b}, R. Sollmann^{c,d}, G. Balme^{e,f}, B.C. Augustine^g, M. Kéry^h, R. Crouthersⁱ, T.N.E. Gray^{i,j}, M. Groenenbergⁱ, S. Prum^k, D.W. Macdonald^a

^a Wildlife Conservation Research Unit, The Recanati-Kaplan Centre, Department of Zoology, University of Oxford, Tubney House, Abingdon Road, Tubney, Abingdon OX13 5QL, UK

^b Panthera, 8 West 40th St., 18th Floor, New York, NY 10018, USA

^c Department of Wildlife, Fish, and Conservation Biology, University of California Davis, Davis, CA, USA

^d Department of Ecological Dynamics, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany

^e Project Pardus, Panthera, New York, NY 10018, USA

^f Institute for Communities and Wildlife in Africa, University of Cape Town, Private Bag X3, Rondebosch 7701, South Africa

^g Department of Natural Resources, Atkinson Center for a Sustainable Future, Cornell University, Ithaca, NY, USA

^h Swiss Ornithological Institute, Sempach, Switzerland

ⁱ World Wide Fund for Nature Cambodia, Street 322, Phnom Penh 12302, Cambodia

^j WWF Tigers Alive Initiative, Phnom Penh, Cambodia

^k Ministry of Environment, 48 Samdach Sihanouk Blvd., Phnom Penh 12301, Cambodia

ARTICLE INFO

Keywords:

Camera-trap survey
Open population SCR
Panthera pardus
Population dynamics
Population viability analysis (PVA)
Recruitment
Southeast Asia
Survival

ABSTRACT

Poaching, a major threat to wildlife worldwide, is pushing species toward extinction. To reduce poaching pressure and combat biodiversity loss, improved law-enforcement efforts reportedly are required; the effectiveness of which can be determined through rigorous monitoring of wildlife populations, particularly of endangered large carnivores. In the Eastern Plains Landscape of Cambodia, law-enforcement efforts increased to counter the severe threats from illegal activities; however, it is unknown if these strategies are benefiting the population of the Critically Endangered Indochinese leopard (*Panthera pardus delacouri*), the last large felid population of eastern Indochina. We used open population spatial capture-recapture models to estimate density, survival, per-capita recruitment, and population growth rates of leopard using data from 7 camera-trap surveys conducted over 11 years (2009–2019). We found that the population (a) declined by over 82 % (from 1.5 to 0.3 leopard/100 km²), (b) had low survival probability (0.58) and low recruitment rates (males: 0.04, females: 0.24), and (c) is expected to continue declining. An additional survey in 2021 failed to detect leopard, suggesting the species now is functionally extinct, if not fully extirpated, from the landscape. Over the study period, there was a drastic increase in human activity, with a 20-fold increase in detection frequencies of humans and a 1000-fold increase in lethal-trap encounter rate. The rise in anthropogenic pressures, particularly snaring, appeared to be the primary reason for the leopard decline, indicating the last decade of management interventions was insufficient to conserve the species, which now appears to be extirpated in all of Cambodia, Laos and Vietnam. This has implications for leopard conservation in the wider region, notably that efforts should now focus on populations within the two remaining strongholds. Our results suggest that increases in law-enforcement efforts alone are unlikely to protect wildlife in eastern Indochina; thus, additional strategies are needed to address the region's snaring crisis, including legislative reforms, community engagement, and programs that reduce demand for wildlife meat and products. Long-term studies of remaining Indochinese leopard populations coupled with timely and effective conservation actions are needed to avoid the complete demise of this subspecies.

[☆] Article impact statement: Law-enforcement efforts alone are not sufficient to protect Critically Endangered leopards and other wildlife in eastern Indochina.

* Corresponding author at: Wildlife Conservation Research Unit, The Recanati-Kaplan Centre, Department of Zoology, University of Oxford, Tubney House, Abingdon Road, Tubney, Abingdon OX13 5QL, UK.

E-mail address: rostro.susana@gmail.com (S. Rostro-García).

<https://doi.org/10.1016/j.biocon.2023.110080>

Received 30 June 2022; Received in revised form 2 April 2023; Accepted 11 April 2023

0006-3207/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Anthropogenic pressures are a major threat to biodiversity worldwide (Schulze et al., 2018). Poaching, one of the most pressing global threats to wildlife, can push endangered species to the brink of extinction (Gross, 2018; Ripple et al., 2016), undermining any conservation effort to protect them. To reduce poaching pressure and combat biodiversity loss, increases in law-enforcement efforts reportedly are required, the effectiveness of which can be determined through rigorous monitoring of wildlife populations, particularly of endangered large carnivores (Duangchantrasiri et al., 2016).

At the center of the global wildlife extinction crisis is Indochina (i.e., mainland Southeast Asia and southeastern China), which has experienced unprecedented and increasing anthropogenic pressures that are decimating wildlife populations throughout the region (Hughes, 2017). Poaching is particularly severe in Indochina, where this threat is so pervasive and intense that several areas of largely intact forest have lost most of their former wildlife diversity and abundance (Gray et al., 2021). Although law-enforcement efforts have increased in some areas of the region, the effectiveness of the strategies used is seldom determined. To date, only two studies investigated the effects of increased law enforcement on the conservation of an Endangered species in Indochina, both on tiger (*Panthera tigris*; Duangchantrasiri et al., 2016, Johnson et al., 2016).

The Critically Endangered Indochinese leopard (*P. pardus delacouri*), a genetically distinct subspecies, historically occurred throughout all of Indochina (Rostro-García et al., 2016). However, populations throughout the region have declined, and this subspecies now occupies only 2–6 % of its historical distribution, with surviving populations being fragmented and at low densities (Rostro-García et al., 2019; Rostro-García, 2021). Previous studies have identified three priority sites for Indochinese leopard conservation in Indochina: (i) the Northern Tenasserim Forest Complex on the Thailand–Myanmar border, (ii) Peninsular Malaysia and (iii) eastern Cambodia (Rostro-García et al., 2016).

In Cambodia, the Indochinese leopard has declined dramatically, and now occurs only in about 4 % of its historical range (Rostro-García et al., 2019). The only potentially viable population remaining in the country occurs in the Eastern Plains Landscape (EPL), a large protected-area complex located in eastern Cambodia (Rostro-García et al., 2019). Because the leopard is reportedly extirpated from Vietnam and Laos, the population in the EPL represents the last known viable population in all of eastern Indochina (i.e., Cambodia, Laos, Vietnam). Within the EPL, the leopard reportedly occurs only in two adjacent protected areas (PA): Srepok Wildlife Sanctuary (hereafter Srepok) and Phnom Prich Wildlife Sanctuary (PPWS). In 2009, the leopard density within Srepok, the larger of the two, was estimated at 3.6 individuals/100 km² (Gray and Prum, 2012), suggesting it likely contained a relatively high number of leopards. However, recent studies reported a rapid decline in leopard density in Srepok (Rostro-García et al., 2018) and low densities within both PA (Rostro-García, 2021), likely driven by increases in poaching, which already led to the extirpation of tiger in the EPL (O’Kelly et al., 2012). To reverse this decline, more information on the long-term population trend is needed to determine the effectiveness of current management practices, assess the current conservation status of the leopard, and guide conservation actions in the EPL, which now contains the last population of any large felid in all of eastern Indochina. However, reliable assessments of leopard population dynamics in Asia are scarce due to the financial and logistical difficulties of conducting these studies at the required temporal and spatial scales. To date no study has yet investigated long-term population dynamics of leopard in Indochina, which we attribute to a lack of conservation investment on the species in the region.

Demographic or vital rates (e.g., recruitment, survival) are essential to understanding the drivers of population dynamics and quantifying population trends through time, and therefore are critical for species’

conservation (Duangchantrasiri et al., 2016; Karanth et al., 2006). Population dynamics and size can directly be estimated through capture-recapture methods (Royle et al., 2014). In classical open population capture-recapture methods, animal movements, particularly of wide-ranging species, can make it challenging to distinguish between survival and emigration processes, which in turn can bias the estimates of the demographic parameters (Royle et al., 2014). By explicitly incorporating information on the movement and spatial location of an individual into the model, open population spatial capture-recapture (hereafter open SCR) models address this issue and offer a more realistic representation of the ecological processes (Gardner et al., 2018; Royle et al., 2014). Despite their advantages, to date no published study on leopard has used open SCR models.

We used open SCR models to estimate density, survival, per-capita recruitment, and population growth rates of the Critically Endangered Indochinese leopard at a conservation priority site for the subspecies where law-enforcement efforts have been increasing. We used data obtained from 7 systematic camera-trap surveys conducted over 11 years (2009–2019) in the first-ever study of leopard population dynamics in Asia. To corroborate the results, we conducted an additional survey in 2021. In addition, because previous studies revealed a strong effect of humans on daily activity patterns of mammals (Gaynor et al., 2018), we explored leopard activity patterns for each survey year. Our aim was to provide reliable information on leopard population and long-term trend in the EPL, which are critical to assess conservation status and determine the effectiveness of current management practices. We predicted that leopard density in Srepok would have remained stable in response to the increased law enforcement, similar to that observed for tigers in western Thailand (Duangchantrasiri et al., 2016). Our results will assist in determining the effectiveness of improved law enforcement strategies for conserving a big cat in Indochina, and help guide future conservation efforts for the leopard in the region.

2. Materials and methods

2.1. Study area

The study was conducted in two protected areas within the EPL of Cambodia: PPWS (2225 km²), and Srepok (3730 km²), formerly called Monduliri Protected Forest (Fig. 1). The habitat of Srepok is dominated (ca. 70 %) by open deciduous dipterocarp forest in relatively flat terrain, interspersed with small patches of evergreen forests (Rostro-García et al., 2021), while PPWS has a mosaic of open deciduous and closed evergreen and semi-evergreen forest patches. The EPL has a distinct dry season for approximately 6 months (November–April), followed by a pronounced rainy season (May–October). Several villages occur along the northern, western, and southern borders of Srepok, whereas several villages occur within the border of PPWS. Our research was carried out within the core zones of both Srepok (ca. 1900 km²) and PPWS (ca. 500 km²), where human access was restricted (Fig. 1). However, illegal human activities (e.g., logging, poaching) occurred in both core zones during our study (Appendix S7).

2.2. Camera trapping

We obtained records of leopard from 7 systematic camera-trap surveys conducted in Srepok from 2009 to 2019. Camera-trap stations (average: 63 stations/year) were set typically for 3 months during the dry season in the core zone of Srepok (Table 1). In general, each station consisted of a pair of camera traps that operated 24 h/day, placed on opposite sides of a trail to obtain photos of both flanks of detected individuals. Stations were considered operational if at least one camera was functional. Cameras were placed on trees located 2–3 m from the middle of the trail, and motion detectors set to trigger at a height of 40–45 cm above the center of the trail. Stations were usually spaced 2–3 km apart and deployed at locations where leopard signs were found, or

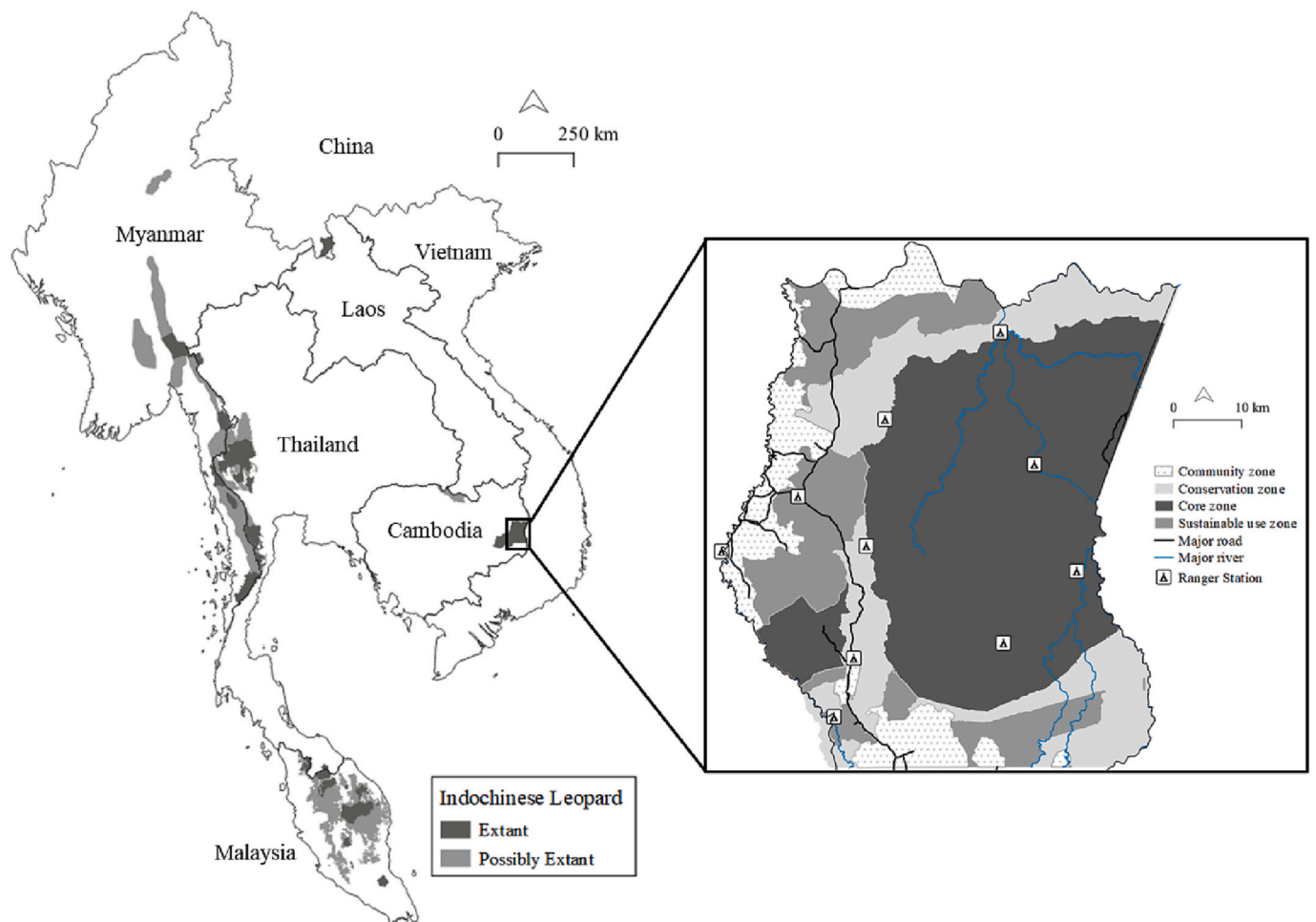


Fig. 1. Current (extant and possibly extant) estimated distribution of the Indochinese leopard (*Panthera pardus delacouri*) in Indochina, modified from Rostro-García et al. (2019). The insert shows the zonation of the study area, Srepok Wildlife Sanctuary, located in the Monduliri Province, Cambodia, and indicates the location of main ranger stations, major roads, and rivers.

Table 1

Summary of Indochinese leopard (*Panthera pardus delacouri*) camera-trap surveys conducted from 2009 to 2021 in Srepok Wildlife Sanctuary, Cambodia. Trap nights represent the total number of days across all functional camera-trap stations (at least 1 operating camera of a pair). F = female, M = male, U = unknown.

Year	Trap nights	No. camera-trap stations	Stations detected	Total no. detections	Mean no. of detections for all individuals (range)	Individuals captured (F, M, U)	Cumulative no. individuals detected
2009	3362	56	38 (67.9 %)	123	10.3 (1–55)	12 (7, 5, 0)	12
2010	902	13	8 (61.5 %)	23	2.3 (1–6)	10 (5, 3, 2)	17
2014	2191	43	13 (30.2 %)	24	3.0 (1–12)	8 (2, 2, 4)	24
2016	2973	46	13 (28.3 %)	23	3.8 (1–11)	6 (3, 2, 1)	30
2017	4314	51	11 (21.6 %)	28	5.6 (1–15)	5 (3, 1, 1)	32
2018	11,612	163	25 (15.3 %)	59	9.8 (1–25)	6 (6, 0, 0)	35
2019	4402	69	12 (17.4 %)	24	6.0 (2–10)	4 (4, 0, 0)	35
2021	1869	58	0	0	0	0	35
Total	31,625	499	120 (27.2 %)	304	–	35 (19, 8, 8)	35

places that maximized chances of encountering leopard (e.g., animal trails, dirt roads).

We identified leopard individuals in photographs based on the unique spot patterns, and sex was determined, when possible, based on secondary sexual traits. For each detection, the same 2 researchers identified individuals from the pelage markings. We created a reference collection of two-sided photos for each individual, and for individuals with only single-sided photos, we used the side with the highest number of records to avoid double counting. We note that the 2009 data set overlapped with that used by Gray and Prum (2012) except that we used data from a larger time frame (2.5 months vs. 2 months).

We also conducted 4 camera-trap surveys for the species in PPWS (2225 km²), using the same methodology described above. However, the number of leopards recorded in PPWS was too low to infer population dynamics. We provide a summary of the leopard data and camera-trapping efforts in PPWS in Appendix S1.

2.3. Analyses

We fitted hierarchical open SCR models in a Bayesian framework (Chandler and Clark, 2014; Gardner et al., 2010; Satter et al., 2019) to estimate combined and sex-specific population parameters of leopard.

Specifically, we aimed to estimate survival probability (ϕ), per-capita recruitment rate (γ), and population growth rate (λ) of leopard in Srepok over the 11-year period, while accounting for non-consecutive survey years, imperfect detection, and activity center relocation between years.

2.3.1. Data structure

We structured our dataset according to a robust design (Pollock, 1982), where each year was a primary period and each day within a survey year a secondary period. The primary period is the unit of time between which demographic changes are assumed to occur. The secondary periods allowed for estimation of yearly closed population abundance in the presence of imperfect detection (Royle et al., 2014; Satter et al., 2019). The detection history was formatted as a three-dimensional array with dimensions $n \times j_{\max} \times T$, where n is the total number of leopards captured across all years, $j_{\max}$ is the maximum number of stations deployed in any year, and T is the total number of years of the study.

2.3.2. Process model

We used the density-independent population growth model described by Chandler and Clark (2014), modified for sex specificity of the parameters (Augustine et al., 2020; Satter et al., 2019). The sex-specific parameters of the model were the female- and male-specific survival probabilities (ϕ^f , ϕ^m), and per-capita recruitment (γ^f , γ^m). We denoted total, female, and male abundance in year t as N_t , N_t^f , N_t^m , respectively. Then, the female- and male-specific abundances in years 2, ..., T were determined by their abundance in the previous year according to $N_{t+1}^f = \phi^f N_t^f + \gamma^f N_t$ and $N_{t+1}^m = \phi^m N_t^m + \gamma^m N_t$, with the total abundance in each year being the sum of the sex-specific abundances. The yearly population densities, in turn, were the abundances divided by the area of the state-space (defined below). Associated with each leopard i in year t were two-dimensional coordinates representing the year-specific activity centers (s_{it}), with the year specificity permitting each leopard to relocate between years (Augustine et al., 2020; Gardner et al., 2010; Royle et al., 2014). We assumed spatial uniformity of activity centers in the first year (Gardner et al., 2018; Satter et al., 2019) across the continuous state-space (S), which represented the area in which the population lived, $s_{i,1} \sim \text{Uniform}(S)$. We defined S by buffering the maximal extent of all traps used across years in the X and Y dimension by at least 4 times the estimated detection-function spatial scale parameter (σ , see below), resulting in a rectangular S . Open SCR requires specification of a model describing movement of the activity centers between primary periods (Gardner et al., 2018). We assumed a Markovian movement model, where activity centers followed a Gaussian random walk across primary periods (Gardner et al., 2018; Royle et al., 2014). We believe this to be an ecologically realistic representation of the spatial population dynamics of leopard in the study area, as individuals likely moved and shifted their activity centers over time due to intrinsic characteristics (e.g., territoriality) and extrinsic factors (e.g., anthropogenic disturbances; Ngoprasert et al., 2017). We truncated the random walk at the limits of the state-space S , which defined the spatial domain of the model, to preclude activity centers from leaving S . Specifically, conditional on the location of activity centers in the first year, the activity centers in primary period $t + 1$ were obtained as draws from a bivariate normal distribution centered on the activity centers in primary period t following $s_{i,t+1} \sim \text{Bivariate Normal}(s_{i,t}, \sigma^T I)$, where I is the identity matrix and σ^T is the year-level spatial scale parameter, which determined how far individuals could relocate. Due to poor mixing of Markov chains of σ^T , likely owing to the sparsity of the data, we did not allow this parameter to vary by sex. The population and transition dynamics were modelled for all 11 years, with these processes being observed in 7 of those years. In years when no survey was conducted, the abundance estimates were obtained from the process model by using the information from the estimated population dynamics parameters and

the estimated population states in adjacent years with surveys (Augustine et al., 2020; Chandler and Clark, 2014).

Preliminary results of the fully sex-specific model indicated that survival was similar between males and females; thus, we fitted a simplified version of the process model described above with a shared survival parameter for both sexes. We report and discuss the results obtained from this simplified version of the model.

2.3.3. Observation model

During each year t , individuals were observed at camera-trap locations X_t over K_t occasions. We recorded observations as binary detection events with a maximum of one detection per station per trap day for an individual leopard and summed detections over occasions. We used a Binomial observation model and assumed the individual trap-by-year number of observations was distributed as $y_{i,j,t}^c \sim \text{Binomial}(p_{i,j,t}^c, K_t)$ for $c \in (f, m)$, where $p_{i,j,t}^c$ are the sex-specific individual-by-trap-by-year detection probabilities. We assumed the detection probabilities were determined by a hazard half-normal detection function conditional on the yearly activity centers, where the sex-specific expected number of counts for individual i at trap location j in year t on each occasion, $\lambda_{i,j,t}^c$, was a decreasing function of the distance between the individual's activity center s_{it} and a trap location x_j : $\lambda_{i,j,t}^c = \lambda_0^c \exp\left(-\frac{\|s_{it} - x_{j,t}\|^2}{2(\sigma^c)^2}\right)$, where λ_0^c and σ^c are the sex-specific baseline detection rate and spatial scale parameters, respectively. We obtained sex-specific detection probabilities by transforming the sex-specific expected number of counts following: $p_{i,j,t}^c = 1 - \exp(-\lambda_{i,j,t}^c)$. We note that we used the Greek letter lambda in three instances: λ for the population growth rate, λ_0^c for the sex-specific baseline detection rate, and $\lambda_{i,j,t}^c$ for the detection rate of individual i of sex c at trap j in year t .

2.3.4. Bayesian inference via data augmentation and Markov Chain Monte Carlo (MCMC)

We augmented the three-dimensional capture history containing the detection frequencies to dimension $M \times j_{\max} \times T$, where $M = 350$ was chosen to be greater than the expected number of individuals ever alive during the 11-year period. To indicate whether leopard i was in the population in year t , we introduced the $M \times T$ matrix z , with entries of 1 indicating that the individual was alive and 0 otherwise. We used this matrix to estimate both population size in every year and population dynamics parameters as described by Chandler and Clark (2014). The observed sex vector C also was augmented to length M , which was used to estimate the sex of uncaptured and sex-indeterminate individuals (Royle, 2009). We introduced a parameter p^{sex} for the probability that any randomly selected individual was a female and assumed the sex of leopard i was distributed as $\text{sex}_i \sim \text{Bernoulli}(p^{\text{sex}})$. We used custom MCMC algorithms from the *OpenPopSCR* R package (Augustine, 2018), vague priors for all population parameters (Chandler and Clark, 2014; Royle et al., 2014; Satter et al., 2019) and sampled from the joint posterior distribution using 20 chains for 250,000 iterations each, thinned by 50, and discarding the first 2500 iterations of each chain as a burn-in. Posterior samples of yearly sex-specific realized abundances were derived following $N_t^c = \sum_i (z_{it} \times I(c_i))$ where I is an indicator function evaluating whether the sex of individual i is male (0) or female (1). We obtained yearly densities by dividing the respective abundance by the area of S , and derived combined and sex-specific realized population growth rates from the appropriate abundance, following $\lambda_t = N_t/N_{t-1}$ and $\lambda_t^c = N_t^c/N_{t-1}^c$ for $c \in (f, m)$ and $t > 1$. The annual realized population growth rate, implied from λ_t estimates, were calculated following $\lambda_f = \sqrt[10]{\lambda_t}$, corresponding to 10 abundance changes over 11 years.

We report results as posterior modes and 95 % highest posterior density intervals (HPDI). For each parameter we calculated the Monte Carlo standard error, considering values $< 5\%$ of the posterior standard

deviation acceptable, assessed chain convergence using the Gelman-Rubin statistic, assuming that values $R < 1.1$ indicated convergence (Gelman et al., 2004), and visually inspected the trace plots.

2.3.5. Population viability analysis (PVA): Forecasting of population size and assessment of extinction probability

We used the fitted model to extrapolate beyond the study years and obtain abundance projections. We predicted expected population sizes 10 years into the future from the last year of survey used in the model (i.e., from 2019 to 2029). In addition, to more closely reflect the trend in the population under study, we obtained the realized population projection conditional on the posterior of z for the final year of data collection. We generated the predictions by taking as input the posteriors of φ , γ^f , γ^m , p^{sex} from MCMC samples, and simulating new values of z based of the fitted open SCR model for 10 years into the future. We did this for each iteration of each chain, and then combined the results to obtain the posterior predicted distribution of realized abundances. From the population trajectory, we estimated time to and probability of quasi-extinction, defined as the probability that the population size fell below a critical threshold, which we considered at 10 individuals, or if individuals of only 1 sex remained. We estimated the posterior probability that the realized population size was <10 individuals, and used the posterior mode and 95 % HPDI of abundance in the projected years as additional indicatives of extinction. To test the predictions from the PVA, we conducted an additional camera-trap survey in 2021 following the same methodology described above.

2.3.6. Activity patterns

We examined leopard activity patterns for each survey year separately, and determined the proportion of the density that occurred between sunrise and sunset (Appendix S2) using the R package ‘overlap’ v.0.3.2 (Meredith and Ridout, 2018).

2.4. Law enforcement, species, and illegal incidents

Because law-enforcement data can provide important information about anthropogenic pressures and efforts implemented to mitigate them, we used data concurrently obtained from the Management Information System (MIST: <http://www.ecostats.com/MIST>) and Spatial Monitoring And Reporting Tool (SMART: <https://smartconservationtools.org/>). We extracted law-enforcement incidents of illegal activity (i.e., snaring) detected by enforcement units during patrolling sessions conducted in Srepok and PPWS from January 2009 to December 2021. We also gathered information about enforcement efforts carried out throughout the years, including number of rangers, kilometers patrolled, and number of lethal traps (e.g., snares, metal snap traps) removed. We calculated lethal trap encounter rate as the number of lethal traps encountered per 100 km patrolled.

In addition, given possible bias and limitations of the enforcement data (Appendix S4), we calculated the detection frequencies of human-related events and mammal species >2 kg for the first and last survey used in the model (i.e., 2009 and 2019). Although in most cases the detection frequencies might not be unambiguously attributed to actual differences in abundance due to the effects of diverse confounding factors (e.g., movement patterns, camera-trap set up, station selection criteria; Sollmann, 2018), we assumed that differences in detection frequencies were associated with differences in abundance given that the same area was surveyed, and cameras were placed along the same roads using similar methodologies. We used detection frequencies as proxies of anthropogenic pressures and their potential effects on mammal species (Appendix S5).

3. Results

The 8 surveys conducted across 13 years (2009–2021) in Srepok

yielded detections of 35 adult leopards (19 females, 8 males, 8 unknown sex) over 31,625 trap nights from 499 camera-trap stations (Table 1). The number of unique individuals detected in any given survey year varied considerably, with the number of recaptures for a given individual within a survey ranging from 0 to 54. Notably, the number of individuals detected declined over the years, from 12 individuals in 2009, to 4 in 2019, and 0 in 2021 (Table 1). Similarly, the number of adult males detected declined over the years, with no males detected from 2018 onwards (Table 1). The proportion of leopard records that occurred during daylight declined throughout the study, ranging from 49 % in 2009 to 8 % in 2019.

Annual survival probability was estimated at 0.58 (95 % HPDI: 0.42–0.70, Table 2), indicating the death of about 42 % of all individuals per year. Annual per-capita recruitment rates were low (<0.25) and estimated to be 86 % higher for females than males (Table 2). Population density declined by 82 % from an estimated 1.5 (1.0–2.4) to 0.3 (0.1–0.5) leopard/100 km² across 11 years (2009–2019; Fig. 2), with no overlap of the 95 % HPDIs between these surveys. Female density estimates were higher than those of males during all years (Fig. 2). Accordingly, estimates of the annual realized sex ratio indicated a female bias over the study period, with the 95 % HPDI not overlapping 0.5 (i.e., equal sex ratio). Detection probability varied by sex, with males being more detectable at their activity center than females ($\hat{\lambda}_0^m = 0.03$; 0.03–0.04; $\hat{\lambda}_0^f = 0.02$; 0.02–0.03), and the detection function spatial scale parameter (σ) being 1.84 times greater in males ($\hat{\sigma}^m = 4.60$ km, 4.18–5.20 km) than in females ($\hat{\sigma}^f = 2.51$ km, 2.28–2.83 km; Table 2). The pooled-sex activity center relocation spatial scale parameter (σ^T) was 4.88 km (3.34–7.48 km) and was difficult to estimate (i.e., low effective sample size) given the sparsity of the data. However, the pairwise correlations of posterior samples for this parameter and survival, female- and male-specific recruitment were low (0.20, –0.21, –0.13, respectively), indicating little influence of the specific numerical value of σ^T (i.e., range covered in the posterior) on estimates of the demographic parameters.

The realized population growth rate over the 11-year period was estimated at 0.14 (0.06–0.33) overall, and 0.16 (0.06–0.40) for females. The annual realized population growth rate assuming constant growth over time was 0.84 (0.77–0.91) overall, and 0.85 (0.77–0.93) for females (no meaningful estimate could be obtained for males due to extinctions in some MCMC draws; see below). Using the estimated realized population growth rates over the 11-year period, the posterior probability that the population was declining (i.e., $\lambda < 1$) was 1.00 for both the overall population and female population. Similarly, the posterior

Table 2

Posterior summaries (mode “Estimate”, standard deviation “SD”, and 95 % highest posterior density intervals “95 % CI”) for the detection and population dynamics parameters obtained using an open population spatial capture-recapture model fitted to camera-trap data of Indochinese leopard (*Panthera pardus delacouri*) from Srepok Wildlife Sanctuary over 11 years (2009–2019), with data collected in 7 of those years.

Parameter ^a	Estimate	SD	95 % CI
λ_0^m	0.032	0.004	(0.025–0.041)
λ_0^f	0.020	0.003	(0.015–0.026)
σ^m	4.596	0.266	(4.175–5.203)
σ^f	2.513	0.141	(2.281–2.832)
γ^m	0.035	0.025	(0.004–0.091)
γ^f	0.241	0.063	(0.121–0.365)
φ	0.582	0.070	(0.423–0.696)
σ^T	4.883	1.098	(3.335–7.477)

^a λ_0 = baseline detection rate, σ = detection function spatial scale parameter, γ = per capita recruitment rate, φ = annual survival probability; σ^T = pooled-sex activity centre relocation spatial scale parameter. Superscripts f and m denote estimates for females and males, respectively.

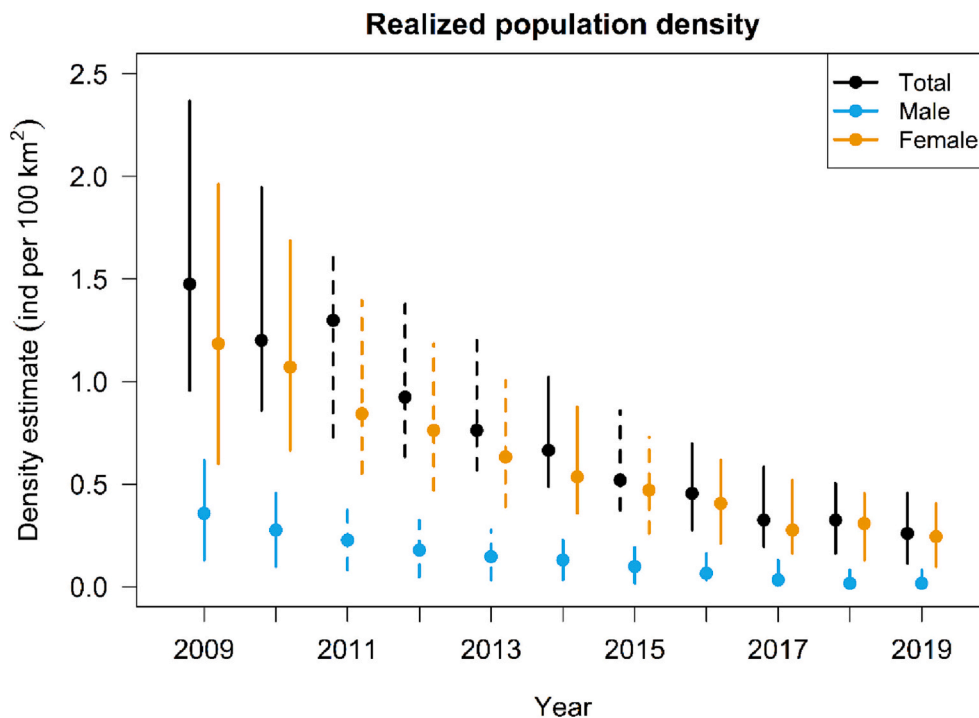


Fig. 2. Total, male, and female realized population density estimates from open population spatial capture-recapture model fitted to camera-trap data of Indochinese leopard (*Panthera pardus delacouri*) in Srepok Wildlife Sanctuary, Cambodia, between 2009 and 2019. Points and lines indicate posterior modes and 95 % highest posterior density intervals, respectively. Solid lines designate years with data collection, whereas dotted lines indicate years without data collection.

probability that the population was declining by $>25\%$ each year (i.e., $\lambda < 0.75$) was 1.00 for both the overall population and female population. Realized population growth rates for males were not calculated because the population dropped to 0 in several iterations/chains, particularly during 2018 and 2019 where the probability of males being extinct was 0.22 and 0.27, respectively.

Considering the estimates of survival and per-capita recruitment, the

associated expected abundances during the years predicted into the future indicated a further decline of the population trajectory (Fig. 3). Similarly, the realized population projection indicated a decline of the population (Fig. 4), with the first population estimate below 10 individuals occurring in 2021 (9.88, 95 % HPDI: 1–24). Our simple PVA suggested that the probability of quasi-extinction by 2029 was 89 %. Alarming, no leopard was detected in the survey conducted in 2021.

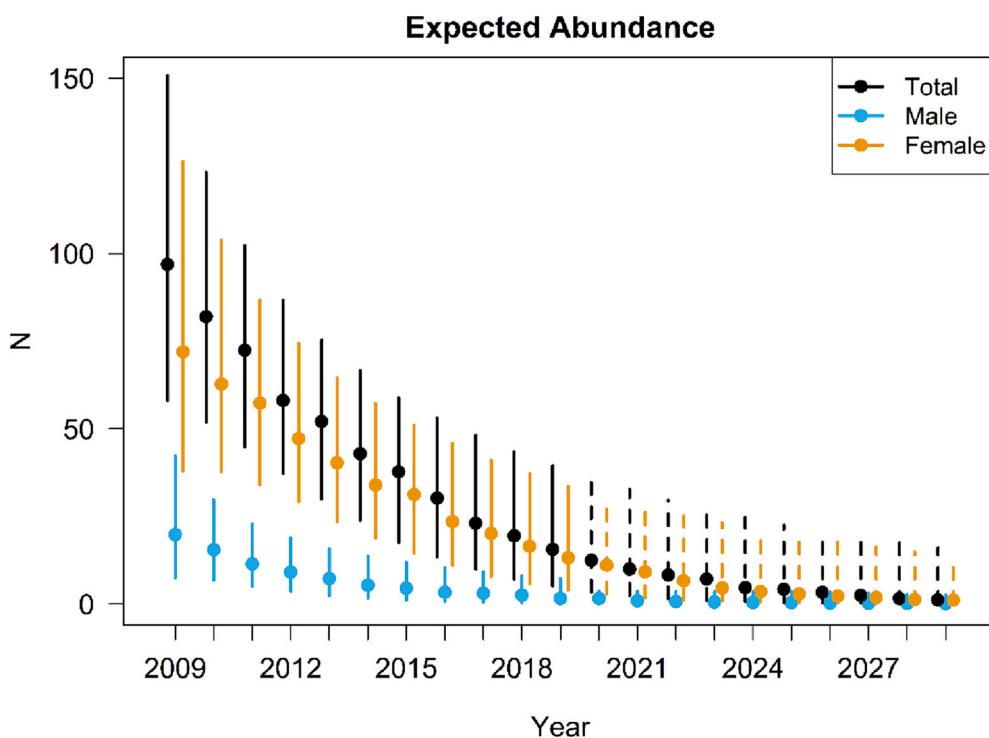


Fig. 3. Total, male, and female Indochinese leopard (*Panthera pardus delacouri*) expected abundance estimates between 2009 and 2019 and projected from 2020 to 2029 for Srepok Wildlife Sanctuary, Cambodia, derived from an open population spatial capture-recapture model fitted to camera-trap data. Points and lines indicate posterior modes of estimates/projections and 95 % highest posterior density intervals, respectively. Solid lines designate years corresponding to the study period, whereas dotted lines indicate years with projections beyond the study period.

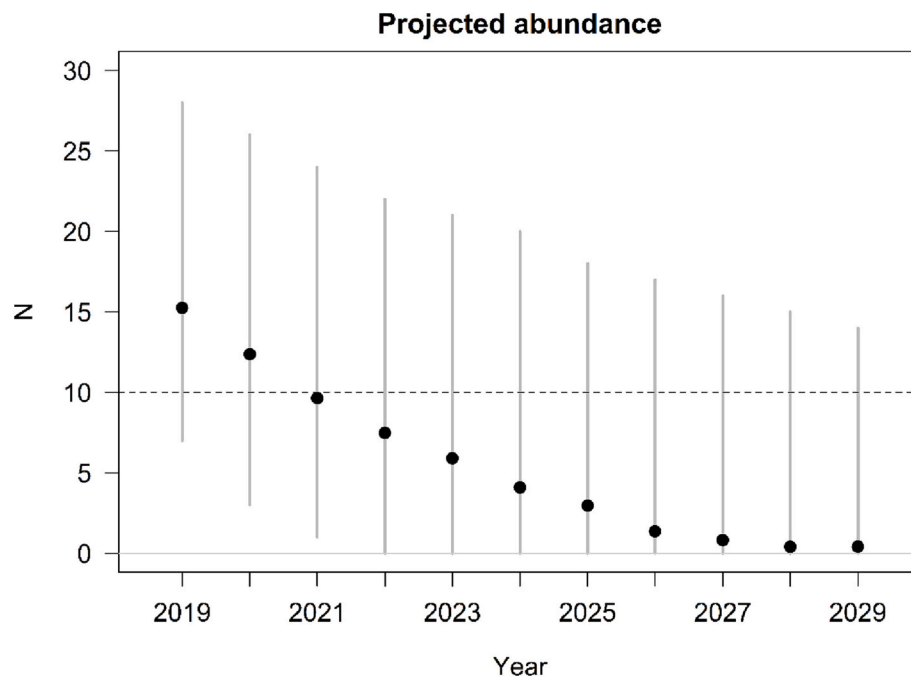


Fig. 4. Population viability analysis (PVA) for the Indochinese leopard (*Panthera pardus delacouri*) population of Srepok Wildlife Sanctuary, Cambodia, with abundance projected 10 years into the future based on our open population spatial capture-recapture model (see text for details). Points and lines indicate posterior modes and 95 % highest posterior density intervals, respectively. Dotted line indicates critical threshold for quasi-extinction (defined as $N < 10$).

In the adjacent PPWS, the number of leopards recorded in 4 surveys conducted across 6 years (2016–2021) declined from 5 to 1 individual, and the detection frequencies of leopard declined at a similar rate (Appendix S1).

3.1. Law enforcement, species, and illegal incidents

Enforcement efforts in the area increased over the entire 13-year survey period, with efforts focused in the core zone, and targeting areas frequently used by leopard and other wildlife. Distance patrolled increased $>3\times$ from 2009 to 2021 (from 19,082 km to 64,630 km), and $>15\times$ from 2012 (lowest annual effort: 4207 km) to 2021 (Table 3). Similarly, the number of rangers increased between 2009 and 2021 (Table 3). Despite increases in enforcement efforts, the number of illegal incidents recorded by the enforcement teams and camera traps increased over time even when standardized by effort. The encounter rate of lethal traps removed in Srepok increased about 1000-fold from 2009 (0.01 lethal traps encountered per 100 km patrolled) to 2021 (10.27 lethal traps encountered per 100 km patrolled; Table 3), being much higher during the second half of the study period (Fig. 5). Human-related events detected by camera traps increased considerably over the study period, with a >20 -fold increase in detection frequencies from 2009 to 2019 (Appendix S5), while the number of mammal species photographed decreased over the study period. Although the number of detected mammal species >2 kg appeared to be similar between 2009 and 2019, there were two mammal species that were not detected in 2019 but that were detected in 2009, greater hog badger (*Arctonyx collaris*) and sun bear (*Helarctos malayanus*). In addition, the detection frequencies of larger species (e.g., banteng *Bos javanicus*, gaur *Bos gaurus*) declined over time, whereas the detection frequencies of some of the smallest or common species (e.g., wild boar *Sus scrofa*, Burmese hare *Lepus peguensis*) increased over time (Appendix S5).

In PPWS, the patterns were similar to those found in Srepok: the number of lethal traps detected by rangers rose dramatically despite increases in enforcement effort (Appendix S3, and S6).

Table 3

Enforcement efforts deployed over 13 years (2009–2021) in Srepok Wildlife Sanctuary, Cambodia. Data on distance patrolled and absolute number of lethal traps detected (e.g., snares and metal snap traps) were obtained from the Management Information System (MIST; 2009–2012) Spatial Monitoring And Reporting Tool (SMART; 2012–2021) and reported by rangers. The encounter rate was calculated as the number of lethal traps encountered per 100 km patrolled.

Year ^a	Number of Rangers ^b	Distance patrolled (km)	Number of lethal traps	Encounter rate
2009	39	19,082	2	0.01
2010	42	31,004	13	0.04
2011	35	27,964	86	0.31
2012	33	4207	0	0.00
2013	49	25,538	254	0.99
2014	21	23,789	556	2.34
2015	23	32,020	1883	5.88
2016	45	39,487	3794 ^c	9.61
2017	38	54,646	1276 ^d	2.34
2018	75	42,809	2105	4.92
2019	80	58,977	2634	4.47
2020	66	82,969	2726	3.29
2021	60	64,630	6637	10.27

^a Information, available from monthly reports, considers yearly data 10 Dec–10 Dec instead of calendar years.

^b Includes Ministry of Environment rangers, police rangers, army rangers, and community rangers. Recruitment of community rangers started in 2017.

^c Intensive targeted snare sweeping campaign implemented by WWF Cambodia and the Ministry of Environment.

^d Enforcement efforts focused on illegal logging.

4. Discussion

By applying open SCR models to an Indochinese leopard camera-trapping data set spanning 11 years, we were able to estimate population demographic parameters, which provided us with a better picture of the population status and trend of this Critically Endangered subspecies in a conservation priority site. Alarming, despite the increase in law-enforcement efforts, the leopard population declined dramatically,

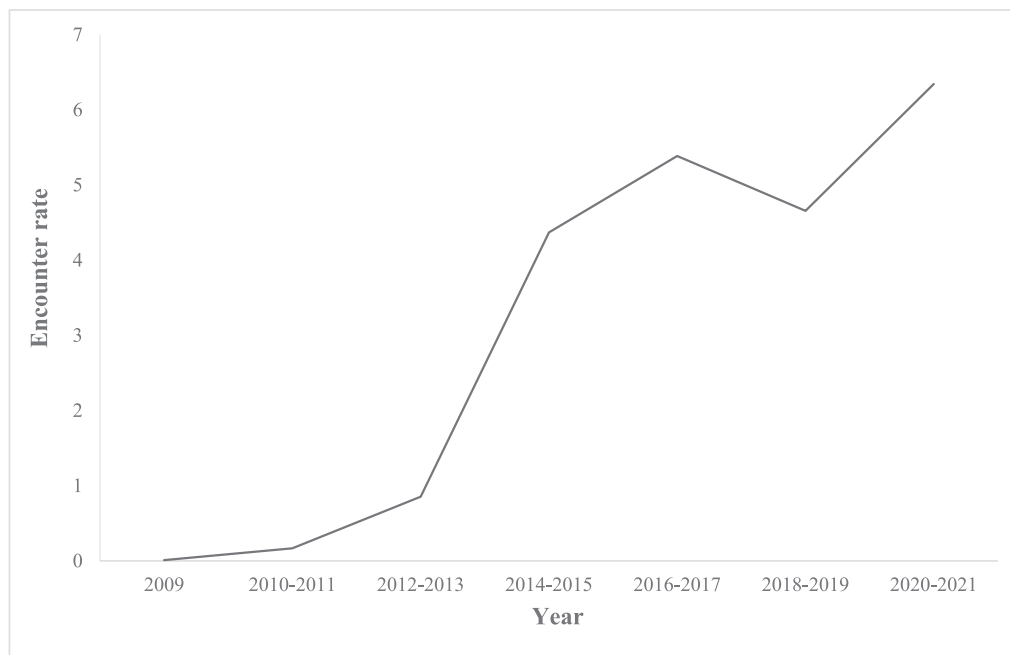


Fig. 5. Lethal trap encounter rate, calculated as the number of lethal traps (e.g., snares and metal snap traps) encountered and removed per 100 km patrolled, between 2009 and 2021 in Srepok Wildlife Sanctuary, Cambodia.

which did not support our prediction. Specifically, our findings suggest an extremely grim situation for the leopard in eastern Cambodia by showing that (a) individuals had a low survival probability and low recruitment rates, (b) the population declined by 82 % over 11 years, and (c) the population trajectory is expected to continue declining and suggests imminent extirpation, which was supported by the lack of leopards detected in 2021.

The estimated survival probability was low and indicated the loss of about 42 % of all individuals, and thus an estimated turnover of almost half of the population per year. Similarly, per-capita recruitment rates were low, and indicated that male recruitment was lower than female recruitment. Because we provided the first estimates of per-capita recruitment for leopard, we are unable to compare our estimates to previous studies. Nevertheless, we hypothesized that higher female recruitment could be due to sex-specific dispersal and survival to adulthood. Female leopards tend to exhibit philopatry and typically have smaller home ranges than sympatric males (Balme et al., 2017; Fattebert et al., 2015). In contrast, males tend to disperse further, and range over larger areas compared to females, exposing males to greater anthropogenic risks (e.g., higher chance of being caught in a lethal trap; Balme et al., 2010; Rostro-García, 2021). Indeed, the activity centers of recaptured individuals suggested that female leopards were mostly philopatric in Srepok. Although the preliminary sex-specific model did not reflect any differences in survival probability between the sexes, it is likely that we had insufficient data for males to draw stronger inferences. However, we suspect a higher mortality of males, owing to the inverse relationship between survival and dispersal distance (Bonte et al., 2012), which in turn presumably caused the lower male recruitment and skewed sex ratios observed. Importantly, the leopard population in Srepok likely was particularly sensitive to mortality, as it appears to be isolated from the neighboring subpopulation in adjacent PPWS (a paved highway separates both PA, and no leopard was detected moving between them), making compensation by immigrants unlikely.

To date only a few studies have investigated leopard population trends over >3 years; most of which have been conducted in southern Africa where both ecological and anthropogenic circumstances are considerably different from those in Indochina. For instance, the leopard population in Phinda Private Game Reserve, South Africa, was reported

to have increased 56 % in a 4-year period due to management interventions (Balme et al., 2009). Only a study in the Soutpansberg Mountains, South Africa, reported a 66 % decline in leopard density from 2008 to 2016, which appeared to be due to illegal human activity (Williams et al., 2017). To our knowledge, the density decline observed during our study is the largest ever documented for the species, and suggests this leopard population currently is well below potential carrying capacity, particularly considering the habitat and prey available. Ecologically similar sites in deciduous forests in India and Nepal have reported leopard densities ranging from 4 to 13 individuals/100 km² (Kalle et al., 2011; Mondal et al., 2012; Thapa et al., 2014), or about 20–65 times higher than the density we estimated at the end of our study.

It is unlikely that changes in abundance found during our study were caused by differences in methodologies because during most years we surveyed approximately the same area of the inner core of Srepok, the most inaccessible and remote part of the park, using the same methods and study design. Similarly, it is unlikely that the differences were caused by insufficient prey numbers, as the detection frequencies of muntjac (*Muntiacus vaginalis*) and wild boar, the preferred and accessible prey of the leopard in Srepok, respectively (Rostro-García et al., 2018), remained relatively stable or increased in the inner core of Srepok from 2009 to 2019 (Appendix S5). Furthermore, line-transect surveys carried out from 2010 to 2020 by WWF Cambodia in both Srepok and PPWS, showed that wild boar densities remained relatively stable in the EPL, whereas muntjac densities only decreased after 2016 (Groeneweg et al., 2020). However, the leopard population had already declined 72 % by 2014; thus, prey numbers likely were sufficient to sustain the leopard population in Srepok, especially considering the adaptability in leopard feeding behavior in the area (Rostro-García et al., 2018). The observed decline of the leopard population years before ungulates began to decline in the EPL likely was due to three main reasons: 1) initial population size, 2) home range size and behavior, 3) intrinsic growth rate. The initial population size of leopards is lower than that of their prey, particularly muntjac and wild boar. In addition, the larger home ranges and wide-ranging movements of leopards increases the probability of individuals being captured by a lethal trap compared to small and medium-sized ungulates which have smaller home ranges. Finally,

leopard intrinsic growth rate, which is about 15 % (Balme et al., 2009), is considerably lower than that of their prey (31–63 %; Bieber and Ruf, 2005; Steinmetz et al., 2010), making it more difficult for leopards to recover from human-caused mortalities compared to sympatric ungulates (Chapron et al., 2008; Kragt et al., 2020).

The primary cause for the precipitous decline of the leopard population in Srepok appeared to be the dramatic increase in anthropogenic pressures, notably poaching. Correspondingly, our camera-trap data showed that there was a drastic increase in human activity over the study period, with a 20-fold increase in detection frequencies of illegal events over a decade (i.e., 2009–2019; Appendix S5). With the depletion of wildlife in China and Vietnam, poaching has intensified in Cambodia (Harrison et al., 2016), predominantly fueled by the illegal wildlife trade and the insatiable demand for wildlife meat, body parts, and products. Although poaching is difficult to detect, and suffers from imperfect and varying detection (e.g., based on patrolling effort and strategy; Ibbett et al., 2020b; O’Kelly et al., 2018), the number of lethal traps clearly increased over the years in Srepok, from being rarely detected at the beginning of the study, to a 1000-fold increase in encounter rate by the end of our study (Fig. 5, Appendix S4). This dramatic increase in the lethal trap encounter rate happened against a backdrop of increased number of rangers and patrolling distances in Srepok during our study (Table 3). Alarming, the reported numbers of snares likely was a vast underrepresentation of the reality on the ground, as up to 80 % of snares can remain undetected by rangers (Ibbett et al., 2020b; O’Kelly et al., 2018). The rise of anthropogenic disturbances likely explains the shift in leopard activity patterns from cathemeral to nocturnal during the study period. A previous study in Thailand revealed a strong effect of humans on daily activity patterns of leopard, which became more nocturnal when human activity increased (Ngoprasert et al., 2017), and the same was likely true for leopard in Srepok, where anthropogenic pressures were mostly diurnal. Thus, our results suggest that humans not only negatively impacted leopard density but also its activity patterns. In PPWS, the patterns were similar to those found in Srepok: number of leopards and overall leopard detections substantially decreased across a 6-year period, during which the number of lethal traps detected by rangers in PPWS rose dramatically despite increases in enforcement effort (Appendix S1, S3, and S6).

One of the major drivers of poaching in eastern Indochina is the high demand for wildlife meat, often regarded as a delicacy or a status symbol by middle- and upper-class urban consumers (FFI Cambodia, 2018; Sandalj et al., 2016). Cambodia has a high prevalence of poaching and reliance on wildmeat, with an estimated 83 % of rural households engaged in wildmeat harvesting at least once per year (Nielsen et al., 2018), including in the EPL (Ibbett et al., 2020a). Multi-species indiscriminate snaring is the most common method used in eastern Indochina, where large numbers of snares are set to capture animals for the wildmeat trade. Snares, usually made from cable, nylon or wire, are affordable and easy to set, but extremely damaging to vertebrates because of their indiscriminate nature with respects to species, sex or age (Gray et al., 2018), representing a direct and persistent threat to wildlife as they remain operational in the landscape until retrieved (Ibbett et al., 2020b; O’Kelly et al., 2018). Rare, slow breeding species, with low population sizes but high probability of being captured by a snare, such as tiger and leopard, are particularly sensitive to snaring and can go extinct even when patrolling effort is high (Chapron et al., 2008; Kragt et al., 2020). Accordingly, widespread snaring has been identified as the main culprit behind tiger density declines in Indochina (Belecky and Gray, 2020), and their extirpation from eastern Indochina (Johnson et al., 2016; O’Kelly et al., 2012; Rasphone et al., 2019). Although direct evidence of leopard poaching was scant, the bones and skin of at least one leopard poached in Srepok were confiscated in 2010 (Gray, 2013), and several unofficial reports of additional leopards poached in Srepok and adjacent areas were made by local people during our study (authors’ pers. obs.). It is likely that other instances of leopard poaching remained undetected as any captured individual likely was rapidly traded across

the border to Vietnam where demand and prices are high (Anh and Wyatt, 2013). The unprecedented levels of poaching, particularly snaring, likely were induced by a plethora of interrelated drivers, including a rise in wildmeat demand, increases in illegal logging, rapid economic growth and infrastructure development (Appendix S7; Groenenberg et al., 2020).

Although decades of armed conflict and poaching led to the decimation, extirpation, and extinction of some of the diverse and abundant wildlife that historically occurred in the EPL (e.g., tiger and kourprey *Bos sauveli*), this complex still contained one of the most intact fauna assemblages of the region at the time our study commenced (Gray et al., 2012; Gray et al., 2014). However, evidence from the camera-trap data suggests not only leopard but other wildlife numbers were decimated throughout the landscape, most plausibly attributable to the proliferation in snaring. For instance, the detection frequencies of all large (>15 kg) and some medium-sized (5–15 kg) species in Srepok decreased substantially during our study. In fact, sun bears and hog badgers, both reported to be especially sensitive to snaring (Duckworth et al., 2016; Scotson et al., 2018), decreased throughout the study and were not detected during the last surveys. Similarly, by 2020 ungulate densities and biomass in both Srepok and PPWS had declined and were much lower than those of ecologically comparable sites, suggesting that ungulate populations currently are severely depleted in both parks (Groenenberg et al., 2020). Current ungulate densities in Srepok and PPWS are similar to or higher than other areas within the EPL (e.g., Keo Seima Wildlife Sanctuary, Yok Don National Park; Groenenberg et al., 2020), depicting a dire picture for wildlife in the wider landscape. To avoid further irreparable biodiversity losses (Appendix S8) it is vital that management and law-enforcement efforts start using new strategies, particularly to better address the snaring crisis in EPL and throughout Indochina.

4.1. Conservation implications

Our results indicate that the law-enforcement efforts implemented were inadequate, and possibly late, to tackle the threat posed by poaching, and thus to curtail the imminent extirpation of leopard from the landscape. Notably, the levels of snaring, which increased by at least two orders of magnitude during the 13-year study, have surpassed all efforts to reduce this threat at a landscape level. Therefore, our findings suggest that increases in law enforcement (e.g., snare removal, patrol distances, ranger numbers) alone are unlikely to prevent the imminent extirpation of leopard and other wildlife in the EPL. A similar situation occurred for tiger conservation efforts in Laos, where increases in law enforcement funding and effort were insufficient to prevent the proliferation in snaring, which ultimately caused the recent extirpation of tiger (Johnson et al., 2016; Rasphone et al., 2019). In Vietnam, efforts to save the Critically Endangered saola (*Pseudoryx nghetinhensis*) resulted in the removal of >75,000 snares from a park, yet levels of snaring remained so high that the IUCN recommended captive breeding to save the species instead of increased funding for law enforcement (IUCN, 2016). Therefore, it is apparent that, unlike in other regions of the world (Moore et al., 2018), increases in law enforcement alone are unable to prevent the proliferation of snaring and protect wildlife in eastern Indochina, because this approach cannot cope with the market dynamics and complexities of the exploding illegal wildlife trade (Challender and MacMillan, 2014). To protect wildlife within PA of this region, where over 12 million snares are estimated to be present (Belecky and Gray, 2020; Kragt et al., 2020), a broad array of actions is undoubtedly needed, including: 1) wildlife trade must be treated as a serious crime, and systematic, intensified, and more efficient law enforcement regimes must be developed, while effective deterrents (prosecution and conviction) consistently applied; 2) enforcement units must target both snare removal and prevention, with clear legal prohibition of snare use and possession; 3) adequate protected area management and enforced zonation laws are required to ensure that core zones represent areas

optimally free of human disturbances, especially snaring; 4) enforced compliance mechanisms are required, including strengthening of the judicial systems, with legislative reforms that criminalize possession of snares, including materials to build them (Gray et al., 2021); 5) design and implementation of education campaigns, community outreach and engagement of local people is essential to reduce snaring and other illegal activities within PA of the region (Steinmetz et al., 2014); 6) demand reduction efforts (e.g., social marketing, evidence-based behavior change interventions), shown to be more cost-effective than antipoaching enforcement (Holden et al., 2019), are required to reduce consumption of wildlife meat and products by the general public (Doughty et al., 2021) at the provincial, national, and regional levels.

Regrettably, the population status and trajectory of the Critically Endangered Indochinese leopard in EPL suggest that population recovery in this priority site is unlikely to occur, and, in fact, the population already is functionally extinct, if not fully extirpated, from the landscape. Despite the regional importance of this population, the last decade of management interventions was insufficient to tackle the poaching threat and conserve leopard. Consequently, leopards now appear to be extirpated in all of Cambodia, Laos, and Vietnam, following the same fate as tigers in these countries. This has important implications for leopard conservation in the wider region, notably that efforts should now focus on remaining viable populations, particularly those within the two remaining strongholds (i.e., Peninsular Malaysia, and the Northern Tenasserim Forest Complex; Rostro-García et al., 2019). We advocate for long-term studies of the Indochinese leopard in remaining populations, coupled with timely conservation action to avoid their demise elsewhere. Only through the halt of anthropogenic pressures, particularly snaring, and the immediate implementation of effective conservation strategies, can the leopard and other endangered wildlife have any chance of persisting in Indochina.

CRedit authorship contribution statement

S. Rostro-García: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Writing – original draft, Writing – review & editing, Validation, Visualization. **J.F. Kamler:** Investigation, Supervision, Writing – review & editing. **R. Sollmann:** Software, Supervision, Writing – review & editing. **G. Balme:** Funding acquisition, Writing – review & editing. **B.C. Augustine:** Software, Writing – review & editing. **M. Kéry:** Software, Supervision, Writing – review & editing. **R. Crouthers:** Investigation, Writing – review & editing. **T.N.E. Gray:** Investigation, Writing – review & editing. **M. Groenenberg:** Investigation, Writing – review & editing. **S. Prum:** Resources, Writing – review & editing. **D.W. Macdonald:** Funding acquisition, Supervision, Writing – review & editing.

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.

Data availability

The authors do not have permission to share data.

Acknowledgements

We would like to thank collaborating organisations, including WWF Cambodia, Ministry of Environment, and Forestry Administration-Ministry of Agriculture, Forestry, and Fisheries, and their departments in Mondulkiri province (Royal Government of Cambodia). We gratefully acknowledge the support in the field provided by research assistants, WWF Cambodia staff, Srepok and PPWS rangers, and local porters. Funding for field work was provided by Panthera, while SR-G's analyses

and writing was supported by a Foley-Béjar Scholarship, provided by Balliol College, University of Oxford, and a grant to DWM from the Turner-Kirk Foundation.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2023.110080>.

References

- Anh, C., Wyatt, T., 2013. A green criminological exploration of illegal wildlife trade in Vietnam. *Asian J. Criminol.* 8, 129–142.
- Augustine, B.C., 2018. OpenPopSCR, GitHub repository. Retrieved from. <https://github.com/benaug/OpenPopSCR>.
- Augustine, B.C., Kéry, M., Olano Marin, J., Mollet, P., Pasinelli, G., Sutherland, C., 2020. Sex-specific population dynamics and demography of capercaillie (*Tetrao urogallus* L.) in a patchy environment. *Popul. Ecol.* 62 (1), 80–90.
- Balme, G.A., Slotow, R., Hunter, L.T.B., 2009. Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. *Biol. Conserv.* 142 (11), 2681–2690.
- Balme, G.A., Slotow, R., Hunter, L.T.B., 2010. Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the phinda-mkhuzi complex South Africa. *Animal Conservation* 13 (3), 315–323.
- Balme, G.A., Robinson, H.S., Pitman, R.T., Hunter, L.T.B., 2017. Flexibility in the duration of parental care: female leopards prioritise cub survival over reproductive output. *J. Anim. Ecol.* 86 (5), 1224–1234.
- Belecky, M., Gray, T.N.E., 2020. Silence of the Snares: Southeast Asia's Snaring Crisis. WWF International, Gland, Switzerland.
- Bieber, C., Ruf, T., 2005. Population dynamics in wild boar *sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *J. Appl. Ecol.* 42 (6), 1203–1213.
- Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M., Travis, J.M.J., 2012. Costs of dispersal. *Biol. Rev.* 87 (2), 290–312.
- Challender, D.W.S., MacMillan, D.C., 2014. Poaching is more than an enforcement problem. *Conserv. Lett.* 7 (5), 484–494.
- Chandler, R.B., Clark, J.D., 2014. Spatially explicit integrated population models. *Methods Ecol. Evol.* 5 (12), 1351–1360.
- Chapron, G., Miquelle, D.G., Lambert, A., Goodrich, J.M., Legendre, S., Clobert, J., 2008. The impact on tigers of poaching versus prey depletion. *J. Appl. Ecol.* 45 (6), 1667–1674.
- Doughty, H., Oliver, K., Verissimo, D., Lee, J.S.H., Milner-Gulland, E.J., 2021. Using theory and evidence to design behaviour change interventions for reducing unsustainable wildlife consumption. *People Nat.* 3 (2), 469–483.
- Duangchantrasiri, S., Umponjan, M., Simcharoen, S., Pattanavibool, A., Chaiwattana, S., Maneerat, S., Karanth, K.U., 2016. Dynamics of a low-density tiger population in Southeast Asia in the context of improved law enforcement. *Conserv. Biol.* 30 (3), 639–648.
- Duckworth, J.W., Timmins, R., Chutipong, W., Gray, T.N.E., Long, B., Helgen, K., Wilcox, D.H.A., 2016. *Arctonyx collaris*. In: The IUCN Red List of Threatened Species 2016: e.T70205537A45209459.
- Fattebert, J., Balme, G., Dickerson, T., Slotow, R., Hunter, L., 2015. Density-dependent natal dispersal patterns in a leopard population recovering from over-harvest. *PLoS ONE* 10 (4), e0122355.
- FFI Cambodia, 2018. Exploring bushmeat consumption behaviors among Phnom Penh citizens. In: Fauna and Flora International, Internal Report.
- Gardner, B., Reppucci, J., Lucherini, M., Royle, J.A., 2010. Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. *Ecology* 91 (11), 3376–3383.
- Gardner, B., Sollmann, R., Kumar, N.S., Jathanna, D., Karanth, K.U., 2018. State space and movement specification in open population spatial capture–recapture models. *Ecol. Evol.* 8 (20), 10336–10344.
- Gaynor, K.M., Hohnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. *Science* 360 (6394), 1232–1235.
- Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. *Bayesian Data Analysis*, (Second Edition ed.). Chapman and Hall/CRC, Boca Raton, Florida, USA.
- Gray, T.N.E., 2013. Activity patterns and home ranges of indochinese leopard *Panthera pardus delacouri* in the Eastern Plains landscape Cambodia. *Nat. Hist. Bull. Siam. Soc.* 59, 39–47.
- Gray, T.N.E., Prum, S., 2012. Leopard density in post-conflict landscape, Cambodia: evidence from spatially explicit capture–recapture. *J. Wildl. Manag.* 76 (1), 163–169.
- Gray, T., Ratanak, O., Keavuth, H., Pin, C., Maxwell, A., 2012. The status of large mammals in eastern Cambodia: a review of camera trapping data 1999–2007. *Cambodian J. Nat. Hist.* 2012, 42–55.
- Gray, T., Vidya, T.N.C., Potdar, S., Bharti, D.K., Sovanna, P., 2014. Population size estimation of an asian elephant population in eastern Cambodia through non-invasive mark-recapture sampling. *Conserv. Genet.* 15, 803–810.
- Gray, T.N.E., Hughes, A.C., Laurance, W.F., Long, B., Lynam, A.J., O'Kelly, H., Wilkinson, N.M., 2018. The wildlife snaring crisis: an insidious and pervasive threat to biodiversity in Southeast Asia. *Biodivers. Conserv.* 27 (4), 1031–1037.

- Gray, T., Belecky, M., O'Kelly, H., Rao, M., Roberts, O., Tilker, A., KY, 2021. Understanding and solving the South-East Asian snaring crisis. *Ecological Citizen* 4, 129–141.
- Groenenberg, M., Crouthers, R., Yoganand, K., 2020. Population status of ungulates in the Eastern Plains Landscape. In: Srepok Wildlife Sanctuary and Phnom Prich Wildlife Sanctuary, Cambodia. WWF-Cambodia, Phnom Penh, Cambodia.
- Gross, M., 2018. Last call to save the rhinos. *Curr. Biol.* 28 (1), R1–R3.
- Harrison, R.D., Sreekar, R., Brodie, J.F., Brook, S., Luskin, M., O'Kelly, H., Velho, N., 2016. Impacts of hunting on tropical forests in Southeast Asia. *Conserv. Biol.* 30 (5), 972–981.
- Holden, M.H., Biggs, D., Brink, H., Bal, P., Rhodes, J., McDonald-Madden, E., 2019. Increase anti-poaching law-enforcement or reduce demand for wildlife products? A framework to guide strategic conservation investments. *Conserv. Lett.* 12 (3), e12618.
- Hughes, A.C., 2017. Understanding the drivers of Southeast Asian biodiversity loss. *Ecosphere* 8 (1), e01624.
- Ibbett, H., Keane, A., Dobson, A.D.M., Griffin, O., Travers, H., Milner-Gulland, E.J., 2020a. Estimating hunting prevalence and reliance on wild meat in Cambodia's Eastern Plains. *Oryx* 1–11.
- Ibbett, H., Milner-Gulland, E.J., Beale, C., Dobson, A.D.M., Griffin, O., O'Kelly, H., Keane, A., 2020b. Experimentally assessing the effect of search effort on snare detectability. *Biol. Conserv.* 247, 108581.
- IUCN, 2016. Urgent Action Needed to Save Critically Endangered “Asian Unicorn” in Viet Nam and Laos. IUCN Press Release.
- Johnson, A., Goodrich, J., Hansel, T., Rasphone, A., Saypanya, S., Vongkhamheng, C., Strindberg, S., 2016. To protect or neglect? Design, monitoring, and evaluation of a law enforcement strategy to recover small populations of wild tigers and their prey. *Biol. Conserv.* 202, 99–109.
- Kalle, R., Ramesh, T., Qureshi, Q., Sankar, K., 2011. Density of tiger and leopard in a tropical deciduous forest of Mudumalai Tiger Reserve, southern India, as estimated using photographic capture–recapture sampling. *Acta Theriol.* 56 (4), 335–342.
- Karanth, K.U., Nichols, J.D., Kumar, N.S., Hines, J.E., 2006. Assessing tiger population dynamics using photographic capture–recapture sampling. *Ecology* 87 (11), 2925–2937.
- Kragt, M.E., Hay, E., Scheufele, G., Bennett, J., Renton, M., 2020. Predicting the effectiveness of community anti-poaching patrols for conserving threatened wildlife in the Lao PDR. *J. Appl. Ecol.* 57 (2), 320–330.
- Meredith, M., Ridout, M., 2018. Package 'overlap'. In: Estimates of Coefficient of Overlapping for Animal Activity Patterns. R 3.6.1.
- Mondal, K., Gupta, S., Bhattacharjee, S., Qureshi, Q., Sankar, K., 2012. Response of leopards to re-introduced tigers in Sariska Tiger Reserve, western India. *Int. J. Biodivers. Conserv.* 4 (5), 228–236.
- Moore, J.F., Mulindahabi, F., Masozera, M.K., Nichols, J.D., Hines, J.E., Turikunkiko, E., Oli, M.K., 2018. Are ranger patrols effective in reducing poaching-related threats within protected areas? *J. Appl. Ecol.* 55 (1), 99–107.
- Ngoprasert, D., Lynam, A.J., Gale, G.A., 2017. Effects of temporary closure of a national park on leopard movement and behaviour in tropical Asia. *Mamm. Biol.* 82 (1), 65–73.
- Nielsen, M.R., Meilby, H., Smith-Hall, C., Pouliot, M., Treue, T., 2018. The importance of wild meat in the global south. *Ecol. Econ.* 146, 696–705.
- O'Kelly, H.J., Evans, T.D., Stokes, E.J., Clements, T.J., Dara, A., Gately, M., Walston, J., 2012. Identifying conservation successes, failures and future opportunities; assessing recovery potential of wild ungulates and Tigers in eastern Cambodia. *PLoS ONE* 7 (10), e40482.
- O'Kelly, H.J., Rowcliffe, J.M., Durant, S., Milner-Gulland, E.J., 2018. Experimental estimation of snare detectability for robust threat monitoring. *Ecol. Evol.* 8 (3), 1778–1785.
- Pollock, K.H., 1982. A capture-recapture design robust to unequal probability of capture. *J. Wildl. Manag.* 46 (3), 752–757.
- Rasphone, A., Kéry, M., Kamler, J.F., Macdonald, D.W., 2019. Documenting the demise of tiger and leopard, and the status of other carnivores and prey, in Lao PDR's most prized protected area: Nam Et - Phou Louey. *Glob. Ecol. Conservation* 20, e00766.
- Ripple, W.J., Abernethy, K., Betts, M.G., Chapron, G., Dirzo, R., Galetti, M., Young, H., 2016. Bushmeat hunting and extinction risk to the world's mammals. *R. Soc. Open Sci.* 3 (10), 160498.
- Rostro-García, S., 2021. Ecology and Conservation of Critically Endangered Leopard (*Panthera pardus*) in Southeast Asia [Doctoral dissertation]. University of Oxford, Oxford.
- Rostro-García, S., Kamler, J.F., Ash, E., Clements, G.R., Gibson, L., Lynam, A.J., Paglia, S., 2016. Endangered leopards: range collapse of the Indochinese leopard (*Panthera pardus delacouri*) in Southeast Asia. *Biol. Conserv.* 201, 293–300.
- Rostro-García, S., Kamler, J.F., Crouthers, R., Sopheak, K., Prum, S., In, V., Macdonald, D.W., 2018. An adaptable but threatened big cat: density, diet and prey selection of the indochinese leopard (*Panthera pardus delacouri*) in eastern Cambodia. *R. Soc. Open Sci.* 5 (2), 171187.
- Rostro-García, S., Kamler, J.F., Clements, G.R., Lynam, A.J., Naing, H., 2019. *Panthera pardus ssp. delacouri*. In: The IUCN Red List of Threatened Species. <https://doi.org/10.2305/IUCN.UK.2019-2303.RLTS.T124159083A124159128.en>. T124159083A124159128.
- Rostro-García, S., Kamler, J.F., Minge, C., Caragiulo, A., Crouthers, R., Groenenberg, M., Macdonald, D.W., 2021. Small cats in big trouble? Diet, activity, and habitat use of jungle cats and leopard cats in threatened dry deciduous forests Cambodia. *Ecology and Evolution* 11 (9), 4205–4217.
- Royle, J.A., 2009. Analysis of capture–recapture models with individual covariates using data augmentation. *Biometrics* 65 (1), 267–274.
- Royle, J.A., Chandler, R.B., Sollmann, R., Gardner, B., 2014. Chapter 8 - model selection and assessment. In: Royle, J.A., Chandler, R.B., Sollmann, R., Gardner, B. (Eds.), *Spatial Capture-Recapture*. Academic Press, Boston, pp. 219–243.
- Sandalj, M., Treydte, A.C., Ziegler, S., 2016. Is wild meat luxury? Quantifying wild meat demand and availability in Hue, Vietnam. *Biological Conservation* 194, 105–112.
- Satter, C.B., Augustine, B.C., Harmsen, B.J., Foster, R.J., Kelly, M.J., 2019. Sex-specific population dynamics of ocelots in Belize using open population spatial capture–recapture. *Ecosphere* 10 (7), e02792.
- Schulze, K., Knights, K., Coad, L., Geldmann, J., Leverington, F., Eassom, A., Burgess, N. D., 2018. An assessment of threats to terrestrial protected areas. *Conserv. Lett.* 11 (3), e12435.
- Scotson, L., Fredriksson, G., Augeri, D., Cheah, C., Ngoprasert, D., Wai-Ming, W., 2018. *Helarctos malayanus*. In: The IUCN Red List of Threatened Species 2017: e. T9760A123798233.
- Sollmann, R., 2018. A gentle introduction to camera-trap data analysis. *Afr. J. Ecol.* 56 (4), 740–749.
- Steinmetz, R., Chutipong, W., Seuaturien, N., Chirngsaard, E., Khaengkhetkarn, M., 2010. Population recovery patterns of Southeast Asian ungulates after poaching. *Biol. Conserv.* 143 (1), 42–51.
- Steinmetz, R., Srirattanaoporn, S., Mor-Tip, J., Seuaturien, N., 2014. Can community outreach alleviate poaching pressure and recover wildlife in South-east Asian protected areas? *J. Appl. Ecol.* 51 (6), 1469–1478.
- Thapa, K., Shrestha, R., Karki, J., Thapa, G.J., Subedi, N., Pradhan, N.M.B., Kelly, M.J., 2014. Leopard *Panthera pardus fusca* density in the seasonally dry, subtropical forest in the Bhabhar of Terai Arc, Nepal. *Advances in Ecology* 2014, 12.
- Williams, S.T., Williams, K.S., Lewis, B.P., Hill, R.A., 2017. Population dynamics and threats to an apex predator outside protected areas: implications for carnivore management. *R. Soc. Open Sci.* 4 (4), 161090.