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Long-term monitoring of wildlife populations for protected area management in Southeast Asia

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Abstract

Long-term monitoring of biodiversity in protected areas (PAs) is critical to assess threats, link conservation action to species outcomes, and facilitate improved management. Yet, rigorous longitudinal monitoring within PAs is rare. In Southeast Asia (SEA), there is a paucity of long-term wildlife monitoring within PAs, and many threatened species lack population estimates from anywhere in their range, making global assessments difficult. Here, we present new abundance estimates and population trends for 11 species between 2010 and 2020, and spatial distributions for 7 species, based on long-term line transect distance sampling surveys in Keo Seima Wildlife Sanctuary in Cambodia. These represent the first robust population estimates for four threatened species from anywhere in their range and are among the first long-term wildlife population trend analyses from the entire SEA region. Our study revealed that arboreal primates and green peafowl (*Pavo muticus*) generally had either stable or increasing population trends, whereas ungulates and semiarboreal primates generally had declining trends. These results suggest that ground-based threats, such as snares and domestic dogs, are having serious negative effects on terrestrial species. These findings have important conservation implications for PAs across SEA that face similar threats yet lack reliable monitoring data.

KEYWORDS

abundance estimates, black-shanked douc, Cambodia, density surface model, distance sampling, Keo Seima Wildlife Sanctuary, population trends, yellow-cheeked crested gibbon

1 | INTRODUCTION

Biodiversity is declining worldwide as unsustainable human activities drive the degradation and loss of natural habitats and overexploitation of species (Johnson et al., 2017; Leung et al., 2020; Mokany et al., 2020). Global efforts to protect habitats and slow biodiversity decline are structured within the Convention on Biological Diversity (CBD; https://www.cbd.int). The Aichi Biodiversity Targets within the Strategic Plan for Biodiversity 2011–2020 identify protected areas (PAs) as key tools for improving the status of biodiversity; Target

11 outlines explicit targets for PA coverage (CBD, 2010). Historically seen as critical tools for conservation (Margules & Pressey, 2000), PAs provide the most likely refuges for biodiversity in increasingly human-dominated landscapes (Bruner et al., 2001). However, increasing PA size and coverage does not guarantee improved conservation outcomes (Armsworth et al., 2018; Bruner et al., 2004) and in some cases can have perverse consequences such as reduced management capacity across a PA network (Barnes et al., 2018). PAs must be adequately resourced and managed in order to fulfill their potential to maintain viable biological populations in the context of increasing human pressure (Coad, Watson, et al., 2019; Geldmann et al., 2018).

Effective monitoring using appropriate biodiversity indicators is critical for PA managers to make informed decisions and assess conservation actions, thus allowing improved management over time (Dixon et al., 2019). Yet, rigorous longitudinal monitoring within PAs is often lacking (B. B. Hughes et al., 2017), hampering informed decision-making and effective deployment of resources. A lack of monitoring systems and frameworks to assess management effectiveness is common challenge facing PAs; only 9.4% of CBD signatories have assessed half or more of their PAs for effectiveness (Secretariat of the CBD 2020). Assessing PA performance requires well-designed monitoring regimes that provide reliable, informative, and appropriate metrics of biodiversity over time (White, 2019). The critical role PAs play in halting biodiversity decline is emphasized in the Post-2020 Global Biodiversity Framework, which is currently being negotiated to replace the 2011–2020 Strategic Plan and includes quantitative biodiversity targets (CBD, 2020a). Therefore, the ability to assess PA efficacy and link conservation action to species outcomes, for which effective long-term monitoring is essential, will become increasingly important.

Southeast Asia (SEA) is characterized by exceptional faunal diversity and endemism (A. C. Hughes, 2017) yet has the highest rate of increase in extinction risk globally (Hoffmann et al., 2010). This region has the highest percentage of the world's threatened plants, reptiles, birds, and mammals (Sodhi et al., 2010) and one of the highest rates of deforestation globally (A. C. Hughes, 2017). Hunting in particular is an urgent threat (Gray et al., 2017). Increasing demand for wild meat and wildlife products, both domestically and for international trade, is driving unsustainable levels of hunting within SEA's forests (Gray et al., 2018; Harrison et al., 2016; Heinrich et al., 2020). Despite the urgency, there is a paucity of long-term quantitative data on wildlife populations in SEA. In many cases, species of conservation interest lack even a single estimate of population size (Table 1), making it hard to assess the performance of individual PAs and national and regional conservation programs. Empirical data are needed to make evidence-based decisions on PA management, evaluate the impact of past action (Geldmann et al., 2018), and increase the accuracy and utility of global assessments of status and trends. Understanding how wildlife populations respond to anthropogenic pressure is of particular importance in PAs, given their role in safeguarding species' persistence (Watson et al., 2014).

In this paper, we present 10 years of wildlife population monitoring from Keo Seima Wildlife Sanctuary (KSWS) in Cambodia, a globally important site for several species (Nuttall et al., 2017), to help address the knowledge gap created by the lack of empirical data on wildlife populations in SEA. Many of the species in our study lack a single reliable population estimate from anywhere else in their range (Table 1). We provide abundance estimates for 11 species within KSWS between 2010 and 2020 and model their population trends over time. We also provide spatial distributions for seven of the species, for which adequate data were obtained. Our study is among the first in the literature to report long-term wildlife population trends with absolute estimates from SEA. We highlight the importance of these results for SEA and International Union for the Conservation of Nature (IUCN) Red List status assessments and for evaluating conservation action and future conservation decision-making in KSWS. Finally, we discuss the need for long-term monitoring in PAs and the implications of our results for conservation programs across SEA.

2 | METHODS

2.1 | Study site

KSWS (*12.3346, 106.8418*, formerly Seima Biodiversity Conservation Area and Seima Protection Forest) falls within Mondulkiri and Kratie provinces in eastern Cambodia. It has an area of 2927 km^2, sharing its south-eastern edge with Vietnam (Figure 1). Our 1880 km^2 study area is the former core zone (Figure 1). KSWS is characterized by a diverse mosaic of habitats; the south-eastern area extends into the Southern Annamite Mountain Range with higher altitudinal mountainous topography and dense evergreen and semievergreen forest (Evans et al., 2013). The central and western areas form the edge of the Eastern Plains Landscape, dominated by low altitudes and dry deciduous dipterocarp forests (Evans et al., 2013; O'Kelly et al., 2012). Complementing the altitudinal and habitat gradients are seminatural grasslands and seasonal and permanent

TABLE 1 Existing population estimates that account for imperfect detection and quantify uncertainty from peer-reviewed literature[a] and the global status of the 11 species monitored in Keo Seima wildlife sanctuary (KSWS)

Common name	Scientific name	In-text abbreviation	IUCN Red List status and global trend	Known threats (entire range)[b]	Locations of population estimates[c]	Density (unit/km^{-2})[d]	Source
Southern yellow-cheeked crested gibbon	*Nomascus gabriellae*	Gibbon	EN ↓	Hunting (trade) Habitat loss and degradation	KSWS, Cambodia Chu Yang Sin NP, Vietnam Cat Tien NP, Vietnam	0.6–0.9 ind 0.3–0.4 grp 0.5–1.0 grp	Rawson et al., 2009 Thinh et al., 2016 Thinh et al., 2018
Black-shanked douc	*Pygathrix nigripes*	Douc	CR ↓	Hunting (traditional medicine, consumption) Habitat loss and degradation	—	—	—
Germain's silver langur	*Trachypithecus germaini*	Langur	EN ↓	Hunting (trade, traditional medicine) Habitat loss and degradation Dam construction	—	—	—
Long-tailed macaque	*Macaca fascicularis*	LT macaque	VU ↓	Hunting (trade, biomedical, consumption, sport) Habitat loss and degradation	Baluran NP, Java, Indonesia	23.0–74.4 ind	Hansen et al., 2019
Northern pig-tailed macaque	*Macaca leonina*	PT macaque	VU ↓	Habitat loss and degradation Hunting (trade, consumption, traditional medicine)	—	—	—
Stump-tailed macaque	*Macaca arctoides*	ST macaque	VU ↓	Habitat loss and degradation Hunting (trade, consumption, traditional medicine, sport)	—	—	—
Banteng	*Bos javanicus*	Banteng	EN ↓	Hunting (consumption, trade, trophy) Habitat loss and degradation Genetic diversity	Phnom Prich WS and Srepok WS, Cambodia KSWS, Cambodia (wild cattle combined) Malua Forest, Borneo Tabin Forest, Borneo	0.7–1.2 ind 0.1–0.8 ind 0.002–0.02 ind 0.005–0.02 ind	Gray et al., 2012 O'Kelly et al., 2012 Gardner et al., 2019 Gardner et al., 2019
Gaur	*Bos gaurus*	Gaur	VU ↓	Hunting (consumption, trade, traditional medicine, trophy) Habitat loss and degradation Competition with livestock	Nagarahole NP (Nalkeri), India Nagarahole NP (Arkeri), India Bahdra TR, India	3.5–8.2 ind 0.7–2.7 ind 0.5–4.3 ind 3.2–8.6 ind 0.1–0.8 ind	Madhusudan & Karanth, 2000 Madhusudan & Karanth, 2000

(Continues)

TABLE 1 (Continued)

Common name	Scientific name	In-text abbreviation	IUCN Red List status and global trend	Known threats (entire range)[b]	Locations of population estimates[c]	Density (unit/km^{-2})[d]	Source
				Disease	Trishna WS, India KSWS, Cambodia (wild cattle combined)		Jathanna et al., 2003 Dasgupta et al., 2008 O'Kelly et al., 2012
Northern red muntjac	*Muntiacus vaginalis*	Muntjac	LC ↓	Hunting (consumption, trade)	Bahdra TR, India KSWS, Cambodia Srepok WS & Phnom Prich WS, Cambodia Murree-Kotli Sattian-Kahuta NP, Pakistan	2.3–5.9 ind 1.2–2.5 ind 1.8–2.6 ind 0.2–0.9 ind	Jathanna et al., 2003 O'Kelly et al., 2012 Gray et al., 2012 Habiba et al., 2020
Wild pig[e]	*Sus scrofa*	Pig	LC ?	Hunting (consumption, sport, trade, reprisals for crop damage) Habitat loss and degradation	Pasoh FR, Malaysia KSWS, Cambodia Srepok WS & Phnom Prich WS, Cambodia	16.2–44.7 ind 1.2–3.5 ind 0.6–2.2 ind	Ickes, 2001 O'Kelly et al., 2012 Gray et al., 2012
Green peafowl	*Pavo muticus*	Peafowl	EN ↓	Hunting (consumption, trade) Collection of chicks and eggs Habitat loss and degradation	Yok Don NP, Vietnam Cat Tien NP, Vietnam KSWS, Cambodia Siem Pang WS, Cambodia Huai Kha Khaeng WS, Thailand	0.1–0.6 calling birds 1.4–10.3 calling birds 0.1–0.6 ind Riverine: 1.1–2.7, Non-riverine: 0.2–0.6 0.3–30.0 calling birds	Sukumal et al., 2015 Sukumal et al., 2015 Nuttall et al., 2017 Loveridge et al., 2017 Sukumal et al., 2017

Abbreviations: ↓, Decreasing global; ?, unknown (www.iucnredlist.org); CR, critically endangered; EN, endangered; FR, forest reserve; Ind, individual density; grp, group density; LC, least concern; NP, national park; TR, tiger reserve; VU, vulnerable; WS, wildlife sanctuary.

[a]See Supporting Information for additional references that do not meet the criteria of this table.

[b]Threats taken from the species assessment page on the IUCN Red List of Threatened species (www.iucnredlist.org).

[c]Only estimates derived from methods that account for imperfect detection and estimate some form of error or variance are included. Minimum counts and relative abundance/density are not included. Publications with limited details on methods that prevented an assessment of the type of estimate were not included.

[d]Where available, the 95% confidence range is reported. Where 95% confidence intervals were not available, the range shown is the reported estimate ± (1.96 × SE). Where available, the density of individuals is reported, otherwise density of groups is reported.

[e]List of reported population estimates is not exhaustive.

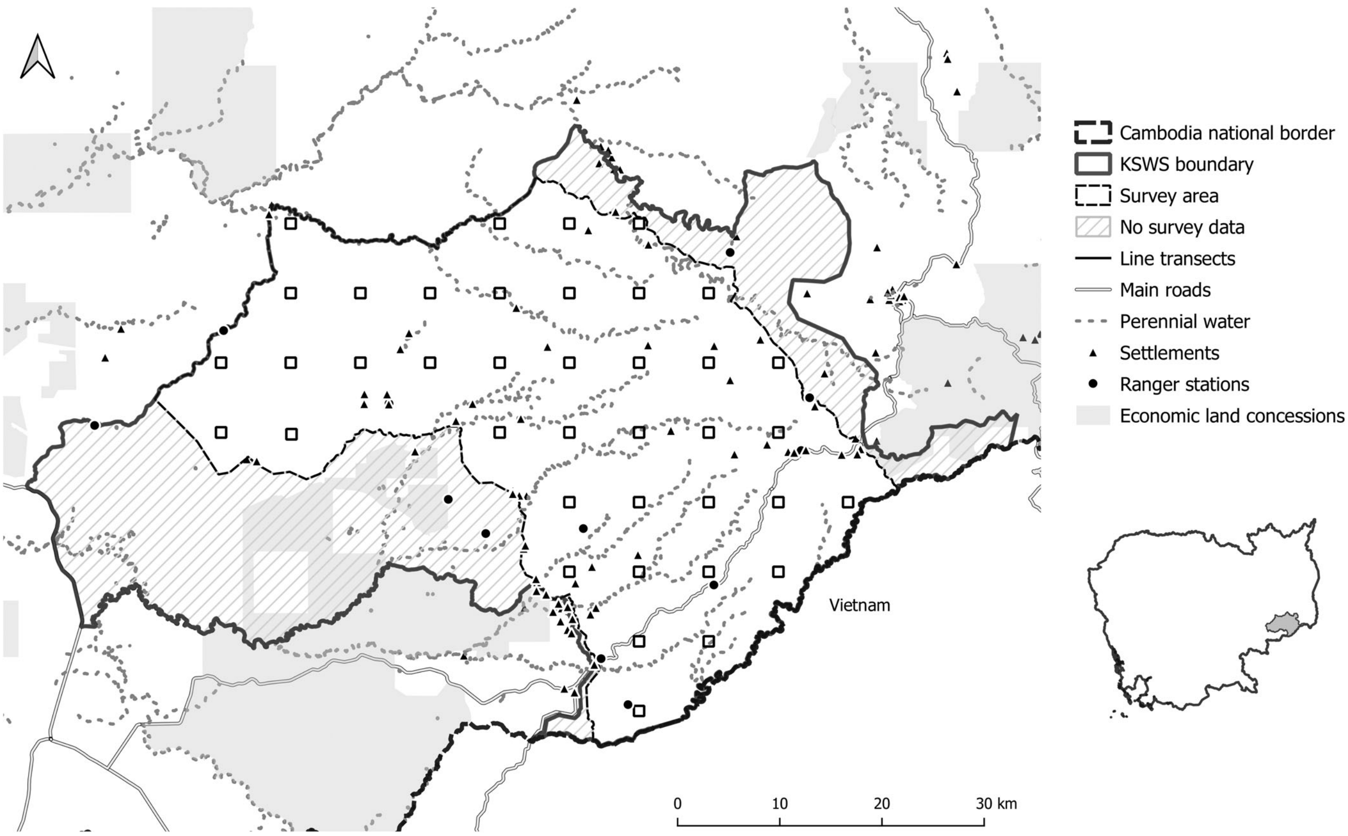

FIGURE 1 Keo Seima Wildlife Sanctuary in eastern Cambodia

water bodies that together support rich biodiversity (Griffin & Nuttall, 2020; Nuttall et al., 2017).

2.2 | Data collection

Data were collected jointly by the Wildlife Conservation Society (WCS) and the Forestry Administration of the Royal Government of Cambodia (RGC) between 2010 and 2016, and by WCS and the Ministry of Environment of the RGC in 2018 and 2020. Forty square line transects of 4 km length were arranged throughout KSWS in a systematic grid with a random start point. Field teams conducted distance sampling surveys along these line transects in 2010, 2011, 2013, 2014, 2016, 2018, and 2020. Teams recorded visual observations of a predefined set of 11 species: those listed as Threatened on the IUCN Red List, easily detected on line transects, or both. The target species were southern yellow-cheeked crested gibbon (*Nomascus gabriellae*, hereafter "gibbon"), black-shanked douc (*Pygathrix nigripes*, hereafter "douc"), Germain's silver langur (*Trachypithecus germaini*, hereafter "langur"), long-tailed macaque (*Macaca fascicularis*, hereafter "LT macaque"), northern pig-tailed macaque (*Macaca leonina*, hereafter "PT macaque"), stump-tailed macaque (*Macaca arctoides*, hereafter "ST macaque"), banteng (*Bos javanicus*), gaur (*Bos gaurus*), northern red muntjac (*Muntiacus vaginalis*, hereafter "muntjac"), wild pig (*Sus scrofa*, hereafter "pig"), and green peafowl (*Pavo muticus*, hereafter "peafowl"). See Table 1 for the target species' global status, threats, and existing population estimates.

Surveys were conducted during the dryer months of December–June. Temporal replication was achieved through multiple visits to each transect within each year. Field teams visited transects for between 1 and 8 days at a time and conducted surveys twice a day, at dawn and dusk. Teams would record only direct visual observations of target species. Laser rangefinders and compasses were used to measure distances and angles from the line transect to detected objects, which constituted either isolated individuals or spatially aggregated individuals (clusters), and cluster sizes were recorded. Distances were measured to the geometric center of clusters. Perpendicular distances from detected objects to the line transect were calculated prior to analysis. Additional data collected for quality assurance and covariate modeling included date, time, observer name, location of observer, and habitat type (2013 onward). Field protocols followed standard line transect methodology outlined in Buckland et al. (2001) and were consistent between years. For further details of field protocols, including testing for bias associated with transect corners, see Supporting Information, O'Kelly et al. (2012), and Nuttall et al. (2017).

2.3 | Annual abundance estimates

We used the conventional distance sampling framework (Buckland et al., 2001) to obtain point estimates of individual density and abundance for each species in each survey year. Only douc had sufficient within-year observations to allow for annual detection functions to be estimated. For the remaining species, distance data from all years were pooled in order to improve the model fit for detection function estimation (Buckland et al., 2001). To account for potential heterogeneity in detection between years, a scaled continuous year variable was tested for all species except douc. We fitted detection function models using the R package distance (Miller, Rexstad, Thomas, et al., 2019; R Core Team, 2017, version 0.9.8). Distance data for all species were truncated to improve model fitting and reduce bias (Buckland et al., 2001). We explored models with uniform, half-normal, and hazard rate key functions and cosine, simple polynomial, and hermite polynomial adjustments, both with and without observation-level covariates (Supporting Information). For further details on density, abundance, and variance estimation in distance sampling, see Buckland et al. (2001, 2004, 2015), Fewster et al. (2009), and Miller, Rexstad, Thomas, et al. (2019).

2.4 | Temporal population trends

We used generalized additive models (GAMs) combined with bootstrapping (Hamilton et al., 2018) to estimate long-term population trends. The original systematic sampling design ensured representative coverage of habitat types, so we employed a bootstrap scheme that would preserve this property (Supporting Information). Each transect was categorized by habitat as either dense or open forest. Transects were sampled with replacement within each category until total within-category effort across all years equaled that of the original data. We fitted detection functions to each set of replicate data and fitted a GAM to the resulting annual abundance estimates to generate a temporal trend curve for each replicate. This process was repeated 2000 times per species. The 50%, 2.5%, and 97.5% quantiles from the replicate GAM curves were extracted pointwise to generate overall population trends and 95% confidence intervals (Fewster et al., 2000). The trend from a single bootstrap replicate was considered positive if the predicted estimate from 2020 was higher than that from 2010 and negative if the opposite was true. The overall trend for a given species was reported as significant if at least 95% of replicates agreed on trend direction; otherwise, the species was classified as stable. Banteng had insufficient observations to support the bootstrap procedure, precluding computation of confidence intervals and trend significance, so a single GAM was fitted to the annual abundance estimates produced from distance sampling analysis.

2.5 | Spatial analysis

We conducted spatial analyses to examine the distribution of each species across KSWS and link relative abundance to spatial covariates. The number of within-year observations for each species was generally low (-Table S2), and so to support the spatial modeling, we combined data from all years into a single analysis, creating a map of relative abundance spanning the whole study period for each species. If a species had fewer than 50 observations from the whole study period, they were excluded from the spatial analysis.

Line transects were partitioned into equally sized, discrete spatial segments, and wildlife observations were allocated to the segment within which they fell. We inspected distance data for all species to identify an appropriate single truncation distance that was used to establish an effective strip width W and subsequent segment size (Buckland et al., 2004). We chose a truncation distance of 50 m which resulted in segments of size 100 m $\times$ 100 m, and between 0% and 27% of observations furthest from the line being discarded. The per-segment abundance was estimated using a Horvitz- and Thompson-like estimator (Buckland et al., 2004) and adjusted for imperfect detection using the species-specific detection function selected in the abundance estimation process above. GAMs were then used to quantify the relationship between the estimated abundance in each segment and the supplied covariates (Buckland et al., 2004; Wood, 2006). For covariate data, we acquired spatial data sets for several environmental and anthropogenic variables that were hypothesized to relate to animal abundance in KSWS. These were within-segment habitat, elevation, distance to water bodies, distance to human settlements, distance to ranger stations, distance to the Vietnamese border, and latitude, and longitude (Supporting Information). The distance to the Vietnam border covariate was included to capture factors such as cross-border wildlife trade and hunting (Harrison et al., 2016).

We ran three groups of models for each species, with each model group assuming a different response distribution (response = number of groups or individuals in a segment): quasi-Poisson, Tweedie, or negative binomial.

TABLE 2 Temporal trends and density and abundance estimates from 2010 and 2020 for 11 species in Keo Seima Wildlife Sanctuary

Species	Replicate agreement (% and direction)[a]	Trend[b]	Density[c] (ind/km^2) [LCI, UCI]		Abundance[c] [LCI, UCI]	
			2010	2020	2010	2020
Yellow-cheeked crested gibbon	89 positive	Stable	0.507 (0.235, 1.093)	0.762 (0.399, 1.455)	952 (441, 2055)	1432 (750, 2735)
Black-shanked douc	88 positive	Stable	12.920 (8.476, 19.692)	13.260 (8.639, 20.354)	24,289 (15,936, 37,021)	24,929 (16,241, 38,266)
Germain's silver langur	54 positive	Stable	1.549 (0.518, 4.634)	0.791 (0.313, 1.999)	2912 (974, 8712)	1487 (588, 3758)
Long-tailed macaque	71 negative	Stable	1.662 (0.733, 3.766)	0.833 (0.421, 1.647)	3125 (1379, 7080)	1566 (792, 3097)
Pig-tailed macaque	97 positive	Increasing	1.068 (0.486, 2.349)	2.090 (1.307, 3.342)	2008 (913, 4417)	3929 (2457, 6284)
Stump-tailed macaque	100 negative	Decreasing	0.281 (0.085, 0.935)	0.122 (0.023, 0.663)	529 (159, 1758)	230 (42, 1246)
Banteng[d]	-	-	0.203 (0.040, 1.040)	-	382 (75, 1956)	-
Gaur	96 negative	Decreasing	0.264 (0.074, 0.946)	0.017 (0.003, 0.095)	497 (139, 1778)	33 (6179)
Northern red muntjac	100 negative	Decreasing	1.800 (1.295, 2.502)	0.439 (0.279, 0.692)	3383 (2434, 4703)	825 (524, 1300)
Wild pig	97 negative	Decreasing	1.796 (0.982, 3.286)	0.585 (0.312, 1.097)	3377 (1846, 6176)	1100 (587, 2063)
Green peafowl	99 positive	Increasing	0.164 (0.082, 0.328)	0.396 (0.199, 0.788)	309 (154, 617)	745 (375, 1481)

Note: Abundance refers to the estimated number of individuals in the study area.

Abbreviations: LCI, Lower 95% confidence interval; UCI, upper 95% confidence interval.

[a]The trend from a single bootstrap replicate was reported as positive if the predicted estimate for 2020 was higher than that for 2010 and negative if the predicted estimate for 2020 was lower than that for 2010.

[b]Overall trend was reported as positive if >95% of the bootstrap replicates were positive and negative if >95% of bootstrap replicates were negative. All trends that did not reach the 95% level were reported as stable.

[c]Density and abundance were estimated using conventional distance sampling, and the analysis was conducted separately from the bootstrapped trend analyses.

[d]There were insufficient observations of banteng in 2020 to produce density and abundance estimates.

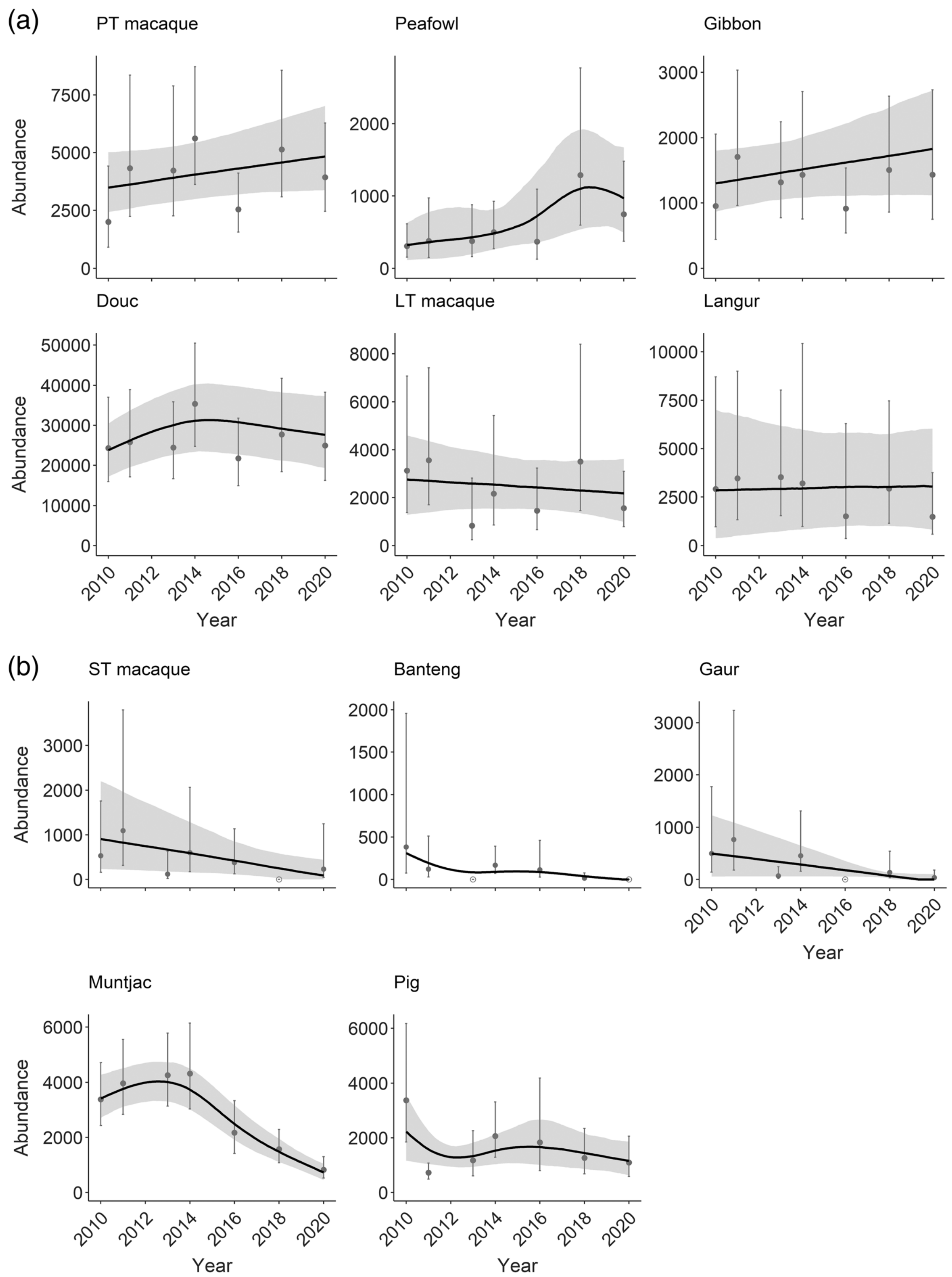

FIGURE 2 Annual abundance estimates (gray points) and population trend (black line) for 11 species in Keo Seima Wildlife Sanctuary between 2010 and 2020. *A* - Species with increasing or stable population trends, *B* - species with declining population trends. Hollow points denote zero observations in that year. Error bars around the annual abundance estimates, and gray error ribbons around the trend lines, denote 95% confidence intervals. Bootstrapping was not possible for banteng and so confidence intervals were not produced. PT macaque = northern pig-tailed macaque, peafowl = green peafowl, Gibbon = southern yellow-cheeked crested gibbon, Douc = black shanked douc, LT macaque = long-tailed macaque, Langur = Germain's silver langur, ST macaque = stump-tailed macaque, muntjac = northern red muntjac, pig = wild pig

We conducted model selection using a combination of diagnostic plot assessment and AIC for Tweedie and negative binomial distributions and analysis of variance for the quasi-Poisson distribution. We retained the habitat variable in all models based on our knowledge of the importance of habitat for the species in this study. Each final model was tested for autocorrelation (see Supporting Information for further details on modeling approach). The selected GAM for each species and a prediction grid with 200 m × 200 m cells were used to predict relative abundance for each species over the study area. Spatial analyses were conducted in the R package dsm (Miller, Rexstad, Burt, et al., 2019).

3 | RESULTS

3.1 | Annual abundance estimates

Effort across all transects and years was 9460 km, resulting in 5056 observations across the study period. The minimum and maximum annual effort was 1260 km (2013) and 1600 km (2010), resulting in 588 and 729 observations, respectively (Table S2). In 2020, the most abundant species among those with increasing populations was PT macaque (estimated abundance 3929 individuals, 95% CI = [2457, 6284], Table 2; encounter rate 0.18 km^{-1}, Table S3), while the least abundant species among those with declining populations was banteng, which was not observed in 2020 (Table 2). The most abundant species overall was douc (estimated abundance 24,929 individuals, 95% CI = [16,241, 38,266], Table 2; encounter rate 1.08 km^{-1} in 2020, Table S3). Cluster size and year were the most frequently retained covariates in the detection function models (six species). Observer and habitat were retained for douc only (Table S3).

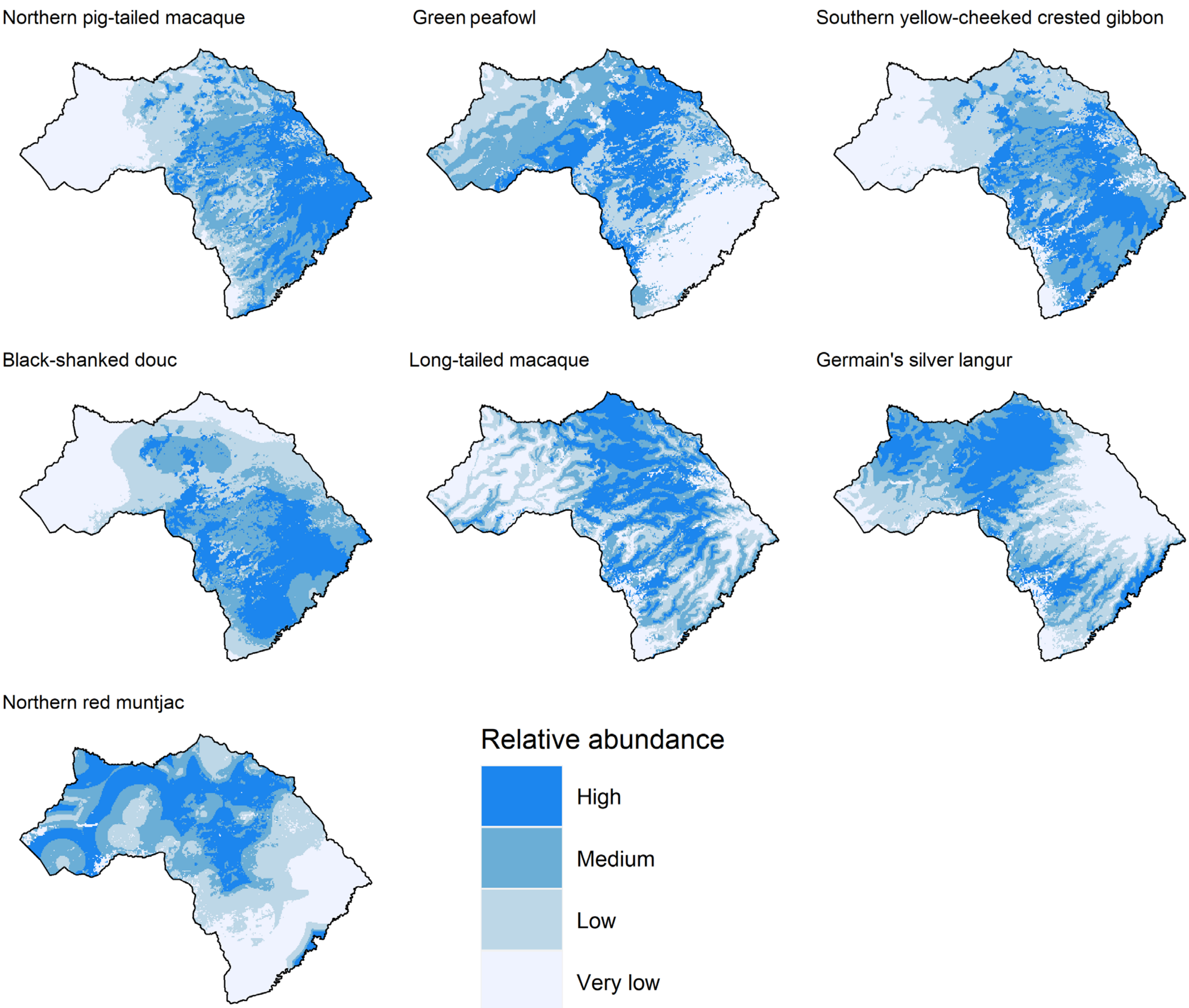

FIGURE 3 Predicted spatial distribution and relative abundance for seven species in Keo Seima Wildlife Sanctuary from the study period in 2010–2020. Relative abundance categories denote predicted species-specific abundance above the 75% quantile ("high"), between the 50% and 75% quantile ("medium"), between the 25% and 50% quantile ("low"), and below the 25% quantile ("very low"). See Supporting Information for corresponding maps of coefficient of variation for the above species

3.2 | Temporal population trends

Significant trends were detected for six species: two positive (PT macaque and peafowl) and four negative (ST macaque, gaur, muntjac, and wild pig; Table 2 and Figure 2). Trends for four species that did not reach 95% directional agreement among replicates were recorded as stable (Table 2). Trend agreement among replicates for ST macaque and muntjac (both negative) was 100% (Table 2).

3.3 | Spatial analysis

Results for banteng, gaur, and ST macaque were excluded because of too few observations. Pig results were excluded because of poor model fit (<5% deviance explained). Final models for the remaining seven species ranged in deviance explained from 16.3% (muntjac) to 66.1% (langur, Table S5). The median coefficient of variation for the spatial predictions for each species ranged from 19% (muntjac) to 125% (langur). Coefficients of variation were high in areas with few or no observations but were generally low (<40%) in areas with high predicted relative abundance (Figure S8).

Distribution and relative abundance were heterogeneous among species (Figure 3). Species with known preference for evergreen and semievergreen forest (gibbon, douc, and PT macaque) had higher predicted relative abundance in the central and southeastern sections of KSWS where this habitat is dominant (Figure 3). Peafowl, muntjac, and langur had highest predicted relative abundance in mosaic habitat and open deciduous forest (peafowl and muntjac: central, north, and northwest; langur: northwest and southwest). Long-tailed macaque had highest predicted relative abundance in areas of KSWS that range from mosaic to open deciduous forest (central and northeast). Distance to the Vietnamese border was the most commonly retained spatial covariate (six species), followed by distance to water and distance to ranger station (five), elevation (four), and distance to settlement (two, Table S5).

4 | DISCUSSION

Long-term monitoring of biological populations is critical for conservation science and policy (B. B. Hughes et al., 2017). Multiyear data sets provide baselines against which conservation efforts can be judged (Magurran et al., 2010) and are important for monitoring PA effectiveness (Geldmann et al., 2018). We have presented population estimates and temporal trends for 11 species over one decade in a large and globally significant PA. These include the first robust estimates for one critically endangered (douc), one endangered (langur), and two vulnerable (PT and ST macaques) primates from anywhere in their ranges. We are aware of only one other study in the literature that presents long-term wildlife population trends in SEA based on absolute abundance estimates rather than uncalibrated indices (Duangchantrasiri et al., 2016; also see Groenenberg et al., 2020). Therefore, our results provide critical information for global status assessments, underpin evaluations of management effectiveness in KSWS, and inform management options in PAs with similar threats regionally.

Spatial modeling indicated that species distributions vary widely, with no clear commonality among species with declining population trends or among those with stable populations. This lack of commonality suggests that population trends are not associated with a particular habitat or area within KSWS but rather are driven by factors associated with species ecology and behavior. The exception is the border with Vietnam, which is a spatial attribute associated with declining abundance. The declining species in our study are ungulates and the single primate that is predominantly ground dwelling, whereas arboreal and semiarboreal primates and peafowl have stable or increasing populations. These results indicate that ground-based threats are likely to be the primary drivers of species decline, in particular implicating snares and free-ranging domestic dogs.

4.1 | Declining populations

Models for all species except langur showed decreased relative abundance closer to the Vietnamese border. Douc, gibbon, and PT macaque prefer evergreen and semievergreen forest (Nadler et al., 2007; Rawson et al., 2009), which dominate the border area. Long-tailed macaque is a generalist occupying a range of habitats (Hansen et al., 2019). Therefore, higher densities would be expected near the border based on habitat characteristics alone. The likely explanation for the contradictory pattern observed is that parts of KSWS in close proximity to the border have been hot spots for illegal cross-border activities throughout the study period, including illegal logging and hunting with firearms and snares (Evans et al., 2013; Ibbett et al., 2020; O'Kelly et al., 2018a). Snare density increases with proximity to the Vietnamese border (O'Kelly et al., 2018b), with high volumes of illegal incursions into KSWS driven by demand for wild meat and wildlife products from Vietnam (Shairp et al., 2016). Snaring is prevalent in Cambodian PAs more generally (Belecky & Gray, 2020; Coad, Lim, & Nuon, 2019). The scale of the snaring problem in a given area is difficult to quantify due to inherent biases in snare removal data resulting from issues with detectability and sampling, although reliable methods have recently been developed (O'Kelly et al., 2018a, 2018b). In 2015, nearly 28,000 snares were removed from Southern Cardamom National Park in southern Cambodia (Gray et al., 2018). In KSWS, 36% of survey respondents reported engaging in hunting and 20% reported laying snares to protect crops (Ibbett et al., 2020). These data suggest that snares may be a primary contributor to regional wildlife population declines.

There is substantial evidence that free-ranging and feral dogs can have negative effects on wildlife populations (J. Hughes & Macdonald, 2013; Young et al., 2011), and these effects are particularly severe in SEA (Doherty et al., 2017). Domestic dogs are commonly used by local communities in Cambodia for hunting inside PAs (Coad, Lim, & Nuon, 2019; Ibbett et al., 2020). In KSWS, 79% of households own dogs and nearly 50% of households take dogs with them into the forest (Ibbett et al., 2020). The number of domestic dogs in KSWS may be as high as 4000, corresponding to 1.36 km^{-2} (Ibbett et al., 2020), which would make the density of domestic dogs several times greater than that of any monitored ungulate. Therefore, it is likely that free-ranging and feral dogs, in addition to widespread snaring, are contributing to declines in ground-based species in KSWS.

The population trend for pig, although exhibiting an overall decline, follows a fluctuating pattern that possibly reflects factors additional to the threats mentioned above. Pigs are highly fecund, and their density-dependent populations can fluctuate dramatically based on food availability and disease (Gentle et al., 2019; Sánchez-Cordón et al., 2019). African swine fever is a plausible contributing factor to pig declines, as the disease has been recorded in Cambodia and can have severe negative effects on wild pig populations (Ikeda et al., 2020; Marinov et al., 2020). Pigs are resilient to relatively high levels of hunting, so the population may be able to rebound quickly if the decline is due to disease or food shortages (Steinmetz et al., 2010).

Although the most prevalent direct causes of wildlife mortality in KSWS are likely to be snares and free-ranging dogs, the broader drivers are more complex. Food insecurity, shifting livelihood strategies, a preference for wild over domestic meat, traditional medicines, targeted hunting by outsiders, increasing debt burdens caused by agricultural and socioeconomic fluctuations, changing perceptions of law enforcement effectiveness, and increased access to local markets are all interacting factors that contribute to hunting of wildlife in KSWS (Ibbett et al., 2020).

4.2 | Stable and increasing populations

We found that gibbon, douc, PT macaque, LT macaque, langur, and peafowl showed stable or increasing population trends. Arboreal primates and birds are less vulnerable than ground-based mammals to hunting with snares and dogs but can be targeted with firearms. The number of firearms in Cambodia has reduced in recent years, and access to firearms has become more difficult (Dyke, 2006). Although some species, including langur and LT macaque, are used in traditional medicine, human consumption of primates is less common in Cambodia than in neighboring Vietnam (Alves et al., 2010). The reduction in firearms and the absence of a strong cultural propensity for primate consumption together may have allowed arboreal primate populations to remain stable. Nevertheless, hunting of primates with firearms, as well as traditional projectile weapons such as crossbows, persists in KSWS (Ibbett et al., 2020), and it is likely to increase if there is continued unregulated movement of people from Vietnam into KSWS with associated illegal hunting and logging activities. The relative scarcity of primates in adjacent Vietnamese PAs means that KSWS has the potential to become a source for the primate trade in Vietnam.

During the study period, there has been large-scale deforestation outside the study area, driven primarily by industrial-scale agriculture in the form of land concessions, and subsequent leakage of illegal land clearance around concessions. In 2010, a Reduced Emissions from Deforestation and Forest Degradation (REDD+) project was initiated in KSWS. This project has provided financial incentives to the RGC and local communities to reduce forest loss in the study area; consequently, forest cover has remained largely intact. An estimated 25,000 ha of forest loss has been avoided because of the REDD+ project (McMahon et al., 2020). Maintenance of forest cover is likely to be another factor supporting stable and increasing population trends for arboreal primates, particularly of gibbon, douc, and langur, which are forest-dependent. Our abundance estimates for douc and gibbon suggest that populations in KSWS are likely to be the largest cohesive populations of these species globally (Duc, Quyet, et al., 2020; Rawson et al., 2020), although for douc, these are the first peer-reviewed abundance estimates published. Abundance estimates for langur suggest KSWS is also a globally important site for this species, although comparison between sites is challenging due to a lack of published population estimates (Duc, Covert, et al., 2020; Moody, 2018).

It is not clear what is causing the apparent difference in trends between LT and PT macaque, but there are several possibilities. Widespread live capture of LT macaques to supplement so-called monkey farms (Lee, 2011) in Vietnam and China, which in turn supply the international biomedical and laboratory trade, is known to have been occurring in Cambodia since 2003 (Eudey, 2008). This practice was reported from the northeast of the country, and specifically in KSWS, from 2006 onward (Lee, 2011; Pollard et al., 2007; Rawson et al., 2007), but there has been little evidence of this practice in KSWS in recent years. A second plausible explanation is the tolerance of LT macaque to a range of habitats, including urban and agricultural areas (Eudey, 2008), which in KSWS will expose the species to a higher density of snares and dogs and opportunistic hunting in parts of its range. PT macaques, although adaptable, prefer dense evergreen and semievergreen forest where available and are therefore less exposed to anthropogenic threats. A decline in LT macaque over time may be reducing resource competition with PT macaque, thus facilitating population increase in PT macaque.

Peafowl are predominantly ground based, yet they have experienced a population increase over the study period. Population recovery of peafowl is rarely recorded in the literature as this species is suffering from habitat loss and hunting across its range, generally leading to population declines (e.g., Sukumal et al., 2015). Nevertheless, when threats are reduced, population recovery can occur (e.g., Sukumal et al., 2017). It is unclear what has caused the increase in peafowl abundance in KSWS. The population density in KSWS is much lower than other areas, even within Cambodia (see Loveridge et al., 2017), suggesting scope for substantial population increases under favorable conditions. Peafowl mortality resulting from ground-based human threats could be lower than that of ungulates for several reasons. They are less vulnerable to dogs, as they can retreat into trees when approached, and they prefer open deciduous habitat, which is found in the central, northern, and western regions of KSWS, out of reach of the Vietnam border and the larger human population centers in the south of KSWS.

4.3 | Implications for Keo Seima Wildlife Sanctuary

KSWS has been officially protected for nearly two decades and over the last decade has benefited from a greater level of conservation investment than most other PAs in Cambodia. KSWS has one of the largest law enforcement teams within any Cambodian PA as well as a range of other programs including indigenous land tenure, community PAs, ecotourism development, and REDD+. Despite operational budgets that are relatively high in the context of Cambodia, the resources available to KSWS managers are well below international benchmarks. For example, KSWS has less than 10% of the recommended law enforcement ratio of one ranger per 5 km^2 (IUCN, 2016). Our results demonstrate that charismatic and ecologically important species are heading rapidly toward local extirpation—trends that are replicated in other Cambodian PAs (Groenenberg et al., 2020). Substantially more investment, particularly into ranger staffing levels, will be required to reverse current species trends. Recent developments in the voluntary carbon markets and Cambodia's decision to support both project and national REDD+ programs suggest this may be achieved in a sustainable manner through REDD+.

Historically, law enforcement efforts in KSWS have been disproportionately focused on illegal logging of luxury timber; this trend has been seen in PAs across the country and was a result of national policies and widespread media attention targeting the economically valuable timber trade. These efforts take place at the expense of combatting wildlife crime, with less attention focused on addressing species declines. Although there have been successes in reducing deforestation compared to the without-project scenario, and an extensive indigenous community land titling program that has increased indigenous tenure within KSWS, there have been no initiatives dedicated to reducing illegal hunting which have focused on community engagement. Community-led law enforcement patrols have been operational in KSWS throughout most of the study period, but these have largely prioritized illegal logging and forest clearance.

The monitoring program in KSWS represents a long-term commitment by RGC and WCS to provide PA managers with rigorous data to inform management action. Our results suggest that for effective conservation management to provide benefits to forests, biodiversity, and communities, increases in scale across all interventions are needed and, within law enforcement, the need for a greater focus on poaching, targeting illegal hunting with snares, weapons, and dogs. Most people in KSWS hunt wildlife for subsistence, as a source of additional income, for medicinal purposes, or to protect crops (Ibbett et al., 2020). Therefore, the community-focused conservation programs within KSWS, which include community engagement and livelihood development, should explore and develop approaches to reduce the community reliance on wild meat, promote domestic sources of protein, improve food security and livelihoods more generally, and offer nonlethal crop protection strategies. Such approaches may be more effective and enduring than law enforcement alone. For detailed management recommendations for KSWS and the Eastern Plains Landscape more broadly, see Griffin and Nuttall (2020) and Groenenberg et al. (2020).

4.4 | Broader implications for SEA

Ten of the 11 species monitored in KSWS are estimated to have declining global populations (Table 1, www.iucnredlist.org), yet our results show that six of these species have stable or increasing populations in KSWS. The remaining five ground-based species have decreasing population trends in KSWS that mirror global population trends. The striking divide we have uncovered between ground-based and arboreal species has important conservation implications for these species throughout their range. Significant declines in KSWS of species such as muntjac, which are generally widespread and common, are concerning as they suggest that sustained anthropogenic pressure can lead to population collapses, even for resilient species. Equally, results for arboreal primates and peafowl from KSWS suggest that when hunting pressure remains low and forest cover is maintained, species populations within a site can remain stable.

Our findings will be valuable for future IUCN Red List assessments and regional conservation planning. We have demonstrated how robust monitoring within KSWS has provided critical information for assessing the impact of past management action, for example, reduced forest loss through the REDD+ program, by linking it to species outcomes such as stable primate populations. Our results can guide future management decisions including increased antisnare efforts and strategic, targeted deployment of resources based on species distributions.

These results also have wider implications for both species conservation and PA management. First, the species trends and potential drivers of population declines seen in KSWS are likely to be replicated in PAs across SEA. Hunting of wildlife for consumption, trophies, and trade is widespread in SEA and has resulted in species extinctions (Brook et al., 2014). Hunting with snares and free-ranging dogs (hunting and feral dogs) in particular represent two of the most serious threats to wildlife populations across SEA. Population declines in terrestrial mammals driven by snaring and free-ranging dogs are likely to be occurring in PAs across SEA where pressure from such threats is high, conservation investment and resources are low, and awareness is limited by inadequate monitoring. In PAs across the region where these threats are known to exist, this study suggests that managers should target resources at antisnare efforts and management of free-ranging dogs to protect populations of terrestrial species.

Second, monitoring biodiversity via appropriate indicators is essential to allow the attribution of species outcomes to conservation action. The establishment of a robust monitoring framework is prioritized in the Post-2020 Global Biodiversity report (CBD, 2020b). Monitoring is particularly important within PAs as their primary function is the conservation of biodiversity. Continued efforts to increase global PA coverage, driven by Aichi Target 11 (CBD, 2010), have seen some success with over 15% of the Earth's terrestrial surface and 7% of oceans legally protected (United Nations Environment Programme World Conservation Monitoring Centre, IUCN, & National Geographic Society, 2020). Yet, evidence linking management action to biodiversity outcomes within PAs is sparse (Geldmann et al., 2018). For PAs where protection of wildlife is a primary objective, long-term data sets on wildlife populations are critical for understanding population dynamics, evaluating extinction risk, informing management action, and assessing interventions (Magurran et al., 2010; White, 2019). Despite the significant contribution that long-term data sets make to conservation research and policy, investment in the collection of such data is falling (B. B. Hughes et al., 2017). There is an urgent need for robust long-term wildlife monitoring data in SEA to understand the effects that hunting, wildlife trade, and other threats are having on already-fragmented populations, to support conservation decision-making and assessment, and ultimately to avoid species extinctions.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

Hannah O'Kelly designed the survey. Hannah O'Kelly, Matthew N. Nuttall, Olly Griffin, Menghor Nut, and Vandoeun Sot conducted different stages of the fieldwork. Matthew N. Nuttall, Olly Griffin, and Rachel M. Fewster conducted the analysis with support from Nils Bunnefeld. Matthew N. Nuttall wrote the manuscript with significant contributions from Nils Bunnefeld, Olly Griffin, Rachel M. Fewster, Philip J. K. McGowan, and Katharine Abernethy.

DATA AVAILABILITY STATEMENT

Raw wildlife data used in this study is publicly available on the Global Biodiversity Information Facility (GBIF) at https://doi.org/10.15468/37thhj. Some raw data are excluded from public access due to their sensitive nature (i.e., locations of threatened species that are vulnerable to hunting) but can be requested from the authors. The R code used for the analysis is available at https://github.com/mattnuttall00/PaperCode_LongTermMonitoringSEA.

ETHICS STATEMENT

This study received ethics approval from the University of Stirling (AWERB/1920/031).

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