Evidence for a major decline of the Endangered large-spotted civet in a former stronghold in eastern Cambodia

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Paper submitted 27 Februrary 2024, revised manuscript accepted 31 July 2024.

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តំបន់ការពារទេសភាពភាគឦសាន្តប្រទេសកម្ពុជាសម្បូរទៅដោយជីវចម្រុះ។ ទោះបីជាការកើនឡើងនៃសកម្មភាពខុសច្បាប់បានជះឥទ្ធិពលអវិជ្ជមានដល់ថនិកសត្វធំៗ ប៉ុន្តែផលប៉ះពាល់លើថនិកសត្វតូចៗមិនទាន់ត្រូវបានសិក្សានៅឡើយ។ នៅឆ្នាំ២០១៩ យើងបានធ្វើការស្រាវជ្រាវដោយប្រើម៉ាស៊ីនថតស្វ័យប្រវត្តិក្នុងដែនជម្រកសត្វព្រៃស្រែពក (SWS) ដើម្បីកំណត់វត្តមាន (occupancy) សត្វសំពោចបីប្រភេទ៖ សត្វខ្ទីន *Viverra zibetha* សត្វសំពោចវល្លិ៍ *Viverricula indica* និង សត្វសំពោចធំ *V. megaspila*។ យើងក៏បានធ្វើការប្រៀបធៀបផងដែរនូវសកម្មភាព (temporal patterns) និងអត្រាកត់ត្រា (encounter rates) សត្វសំពោចទាំងបីប្រភេទនេះនៅឆ្នាំ២០០៩-២០១០។ នៅឆ្នាំ២០១៩ សត្វខ្ទីនមានអត្រាកត់ត្រាខ្ពស់ជាងគេ (encounter rate = 3.28) តាមដោយសត្វសំពោចវល្លិ៍ (2.85) និងសត្វសំពោចធំ (0.73)។ ផ្ទុយទៅវិញ សត្វសំពោចធំមានអត្រាកត់ត្រាខ្ពស់នៅឆ្នាំ២០០៩-២០១០ ដែលអត្រាកត់ត្រានេះមានអត្រាកត់ត្រាទាបជាងសត្វសំពោចប្រភេទផ្សេងទៀត។ ការសិក្សានេះ ដូចទៅនឹងការរកឃើញពីឆ្នាំ២០០៩-២០១០ ដែលសត្វសំពោចទាំងបីប្រភេទនេះធ្វើសកម្មភាពនៅពេលយប់ ហើយបានបង្ហាញពីភាពត្រួតស៊ីគ្នាខ្ពស់នៅឆ្នាំ២០១៩។ តំបន់ទំនាបព្រៃល្បោះស្ងួតដែលគ្រប់ដណ្តប់នៅ SWS មានទំនាក់ទំនងវិជ្ជមានជាមួយ occupancy សត្វខ្ទីន និងសត្វសំពោចវល្លិ៍ ប៉ុន្តែគ្មានទំនាក់ទំនងវិជ្ជមានជាមួយ occupancy សត្វសំពោចធំទេ។ លទ្ធផលនៃការសិក្សារបស់យើងបង្ហាញពីលទ្ធភាពបម្រែបម្រួលគួរឱ្យកត់សម្គាល់នៃពពួកសត្វសំពោចក្នុងរយៈពេលមួយទសវត្សរ៍ចុងក្រោយនេះនៅ SWS និងការថយចុះយ៉ាងគំហុកនៃសត្វសំពោចធំដែលជាប្រភេទសត្វរងគ្រោះ។ សកម្មភាពល្មើស ជាពិសេសការប្រមាញ់ខុសច្បាប់បានកើនឡើងយ៉ាងខ្លាំងនៅកំឡុងពេលចុះសិក្សាដាក់ម៉ាស៊ីនថតស្វ័យប្រវត្តិនៅដែនជម្រកសត្វព្រៃស្រែពក ដែលប្រហែលជាមូលហេតុចម្បងនៃការថយចុះនេះ។

Abstract

The eastern plains landscape of Cambodia is rich in biodiversity, although increases in illegal activities have negatively impacted large mammals whereas the impacts on smaller mammals are unknown. We conducted a camera-trap survey in Srepok Wildlife Sanctuary (SWS) in 2019 to determine the occupancy of three ground-dwelling civets: large Indian civets *Viverra zibetha*, small Indian civets *Viverricula indica* and large-spotted civets *V. megaspila*. We also compared the

CITATION: Toem Y., Pin C., Kamler, J.F., Rostro-Garcia, S., Chou S., Chhin S., Groenenberg, M. & Macdonald, D.W. (2024) Evidence for a major decline of the Endangered large-spotted civet in a former stronghold in eastern Cambodia. *Cambodian Journal of Natural History*, **2024**, 122–133.

temporal patterns and encounter rates of these species to those recorded during a survey in 2009–2010. In 2019, large Indian civets were recorded most (encounter rate = 3.28), followed by small Indian civets (2.85) and large-spotted civets (0.73). In contrast, large-spotted civets had the highest encounter rate in 2009–2010, whereas the rates were much lower for the other civet species. In agreement with findings from 2009–2010, all civet species were primarily nocturnal and showed high temporal overlap in 2019. The lowland deciduous dipterocarp forests that dominate SWS had a positive relationship with the occupancy of large and small Indian civets, but not large-spotted civets. Our results demonstrate the possibility of radical changes in the terrestrial civet community over the last decade in SWS, with a strong possibility of a major decline in the Endangered large-spotted civets. Illegal human activities in SWS, notably poaching, increased dramatically between the surveys and are probably at the root of this apparent decline.

Keywords Cambodia, camera traps, deciduous dipterocarp forest, occupancy modeling, small carnivore, Srepok Wildlife Sanctuary.

Introduction

The eastern plains landscape (EPL) of Cambodia is one of the largest extant deciduous dipterocarp forests (DDF) in Southeast Asia (Tordoff *et al*., 2005). The landscape has supported a wide range of globally threatened species and subspecies, including mammals such as Asian elephant *Elephas maximus*, banteng *Bos javanicus*, gaur *B. gaurus*, Eld's deer *Rucervus eldii*, dhole *Cuon alpinus*, Indochinese leopard *Panthera pardus delacouri*, and large birds such as giant ibis *Thaumatibis gigantea*, white-shouldered ibis *Pseudibis davisoni*, lesser adjutant *Leptoptilos javanicus*, green peafowl *Pavo muticus* and several vulture species (Pin *et al*., 2018; Rostro-García *et al*., 2018; Groenenberg *et al*., 2020; Kamler *et al*., 2020).

Deciduous dipterocarp forests are characterized by an open canopy and grassy understory and currently cover about 15–20% of Southeast Asia (Tordoff *et al*., 2005; Wohlfart *et al*., 2014). However, DDF has become the most threatened of all forest types in the region due to illegal logging and habitat transformation (Wohlfart *et al*., 2014; Pin *et al*., 2018; Rostro-García *et al*., 2021). Additionally, a snaring crisis is devastating wildlife populations in Southeast Asia, especially in Cambodia, Laos and Vietnam (Gray *et al*., 2018). These twin factors of habitat loss and indiscriminate snaring are taking their toll on larger mammal species of Southeast Asia (Gray *et al*., 2021; Groenenberg *et al*., 2023), with the result that most are experiencing rapid declines in numbers and local extirpations. In a microcosm of what is happening at a larger scale throughout Southeast Asia, the EPL has experienced an exponential increase in snaring and other forms of poaching along with widespread illegal logging and habitat transformation during the last decade (Groenenberg *et al*., 2020). Consequently, ungulate populations have decreased dramatically in the EPL (Groenenberg *et al*., 2020, 2023; Nuttall *et al*., 2022), whereas tigers have been extirpated (O'Kelly *et al*., 2012) and Indochinese leopards have become functionally extinct (Rostro-García *et al*., 2023).

While the recent increase in poaching and other illegal human activities in EPL have had severe negative impacts on all large mammal populations, it is not known if small carnivore populations have also been impacted. If small carnivores are not targeted in snaring and other forms of poaching, their populations may not be impacted to the same degree as large mammals (Gray *et al*., 2021; Groenenberg *et al*., 2023). Recent research has shown that the abundance and densities of leopard cats *Prionailurus bengalensis*, a small habitat generalist, are relatively high in EPL (Rostro-García *et al*., 2021; Pin *et al*., 2022). This indicates that they probably have not been severely impacted by recent increases in illegal human activities. In contrast, the abundance of jungle cats *Felis chaus*, a DDF-dependent species in this region, was extremely low (Duckworth *et al*., 2005; Rostro-García *et al*., 2021). This might indicate that species restricted to DDF might be more negatively impacted by illegal human activities in EPL compared to habitat generalists. However, more research is needed on the subject.

Of all small carnivore groups in the EPL, civets are particularly diverse. These comprise at least four species including the semi-arboreal common palm civet *Paradoxurus hermaphroditus* and three ground-dwelling civets: the large-spotted civet *Viverra megaspila*, the large Indian civet *V. zibetha* and the small Indian civet *Viverricula indica*. Large-spotted civets are classified as Endangered by IUCN due to population declines resulting from habitat loss and hunting (Timmins *et al*., 2016b). In contrast, none of the other three civet species have experienced major population declines or have small populations or small geographic ranges. As such, they are classified as Least Concern by IUCN (Choudhury *et al*., 2015; Timmins *et al*., 2016a). Large-spotted civets are associated with forests at lower altitudes (Gray *et al*., 2010; Jennings & Veron, 2011; Hamirul *et al*., 2015) and the EPL, with its vast tracts of lowland deciduous dipterocarp forests, is considered a global stronghold for the species (Gray *et al*., 2010; Timmins *et al*., 2016b). In contrast, all of the other civet species in this area of Cambodia are not restricted to lowland areas and consequently occur across different forest types (Francis, 2008; Jennings & Veron, 2022).

The current status and habitat requirements of civet species in the EPL are unknown. However, camera-trapping surveys conducted for large carnivores in the EPL (Rostro-García *et al*., 2023) have provided important data on the three ground-dwelling civet species. For example, camera-trap surveys conducted in 2009–2010 in Srepok Wildlife Sanctuary, the largest protected area within the EPL, showed that the large-spotted civet had the highest encounter rate and naïve occupancy of these species (Gray *et al*., 2010). This study indicated that large-spotted civets appear to be DDF-dependent in EPL, likely due to its confinement to lowland areas dominated by DDF. In contrast, the other civet species were found across a wider range of altitudes and terrain encompassing various forest types. To determine the current status and habitat use of ground-dwelling civets, we conducted a camera-strap survey in Srepok Wildlife Sanctuary in 2019. We focused on the three ground-dwelling civet species, namely the large-spotted civet, the large Indian civet and the small Indian civet (Fig. 1). We used occupancy analysis to determine the habitat use of these and investigated their activity patterns. We calculated camera-trap encounter rates and naïve occupancy for each species and compared our results to those from 10 years earlier. If camera-trap methodology and other possible confounding variables were comparable between the two surveys, this comparison would allow us to determine any changes in the civet community over the last decade in the EPL.

Fig. 1 From top to bottom, a large-spotted civet *Viverra megaspila*, large Indian civet *V. zibetha* and a small Indian civet *Viverricula indica* in Srepok Wildlife Sanctuary, 2019.

Methods

Study site

Our camera-trap study was conducted in the core zone of Srepok Wildlife Sanctuary (3,729 km^2; 12°50′N, 107°50′E; Fig. 2) within the EPL. This is under the management of the Cambodian Ministry of Environment. Srepok Wildlife Sanctuary (SWS) is categorized into four distinct zones: 1) core zones covering 1,876 km^2, 2) conservation zones (756 km^2) with severely restricted human access by law, 3) sustainable use zones (657 km^2) and 4) community zones (439 km^2) where local communities engage in grazing cattle and subsistence hunting using traditional methods, and collection of non-forest timber products. The sanctuary is part of the Lower Mekong Dry Forest Eco-region within Southeast Asia and borders several other protected areas in Cambodia and Vietnam (Fig. 2). It is predominantly covered by DDF which accounts for over 70% (1,050 km^2) of the area, with smaller patches of mixed-deciduous forest and semi-evergreen forest (SEF) on hilltops and along rivers (530 km^2) (Pin *et al*., 2013; Rostro-García *et al*., 2021). During the dry season, the DDF experiences high-frequency forest fires, which result in extensive open understory vegetation and sparse canopy cover (Pin *et al*., 2013; Kamler *et al*., 2021). There is a distinct dry season from about November to April, with average monthly rainfall ranging from 3 to 121 mm. The rainy season typically spans from about May to October, with monthly rainfall ranging from 248 to 370 mm (rainfall data from nearby Sen Monorom, Cambodia, 1982–2012; climate-data.org; accessed 10 July 2019).

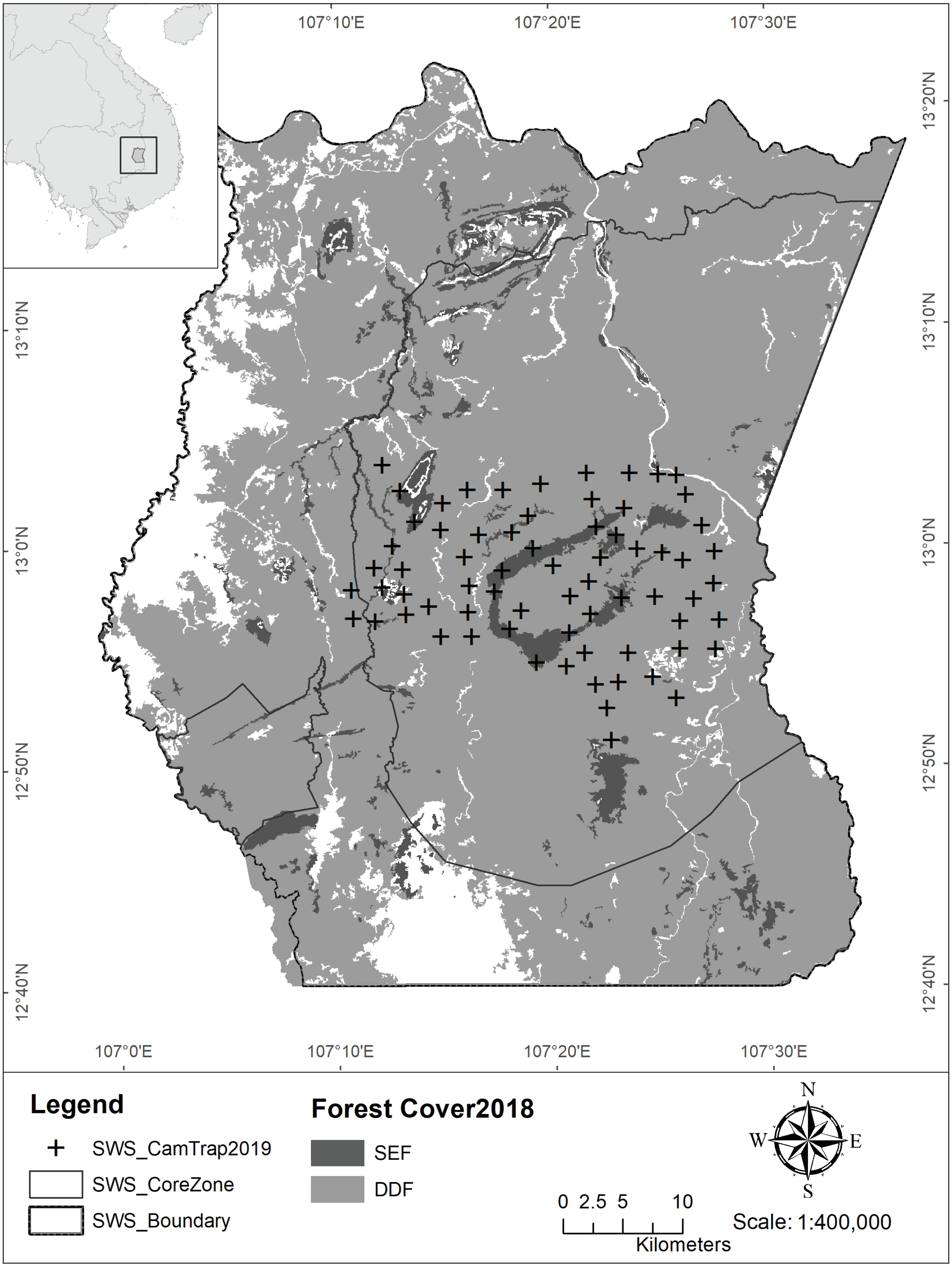

Fig. 2 Distribution of forest types and 69 camera traps used in the 2019 survey in Srepok Wildlife Sanctuary (SWS). The inset map indicates the location of the sanctuary within the broader region.

The wildlife sanctuary supports a globally important banteng population (Gray *et al*., 2012) and several large and medium-sized carnivores, including Indochinese leopards, dholes, sun bears *Helarctos malayanus*, golden jackals *Canis aureus* and jungle cats (Rostro-García *et al*., 2018, 2021; Kamler *et al*., 2020, 2021). It also supports several small carnivores, including leopard cats, yellow-throated martens *Martes flavigula*, small Asian mongooses *Herpestes javanicus*, crab-eating mongooses *H. urva*, and ferret-badgers (*Melogale* sp.) (Rostro-García *et al*., 2021; Pin *et al*., 2022).

Camera-trapping survey

We used records of civets from a camera-trap survey conducted for leopards in the core zone of SWS from 8 February to 8 May 2019 (a total of 4,402 trap nights). The survey employed 69 camera trap stations using three different models of cameras, namely Panthera V6, Reconyx PC900 and Bushnell Trophy. Camera stations were spaced 2–3 km apart along dirt tracks and trails, and were checked once each month until they were collected. Each camera station comprised paired cameras set on opposite sides of the trail. The cameras were attached to trees, positioned 40–50 cm above the ground, at distances of 2–3 m from the centre of the trail. Unbaited cameras were set up in all habitat types present in the core zone, covering an area of approximately 766 km² (Fig. 2).

We compared our results with Gray *et al*. (2010) who conducted camera-trapping during 2009–2010 (December 2009 to June 2010) in the same area of the SWS core zone, also using 69 camera stations (a total of 4,264 trap nights). In that survey, Reconyx RapidFire Professional PC90 cameras were used, but the sampling protocols were otherwise the same e.g., camera stations were set between 2–3 km apart along dirt roads and trails. The camera grid in 2019 covered almost the same area as that used in 2009–10 and both were primarily conducted during the dry season. There was no significant change in vegetation conversion between 2009 and 2019, although the area experienced significant increases in poaching, illegal logging and other human activities (Groenenberg *et al*., 2020; Nuttall *et al*., 2022; Rostro-García *et al*., 2023).

Data analysis

Management of camera-trap photos from 2019 was undertaken with the DigiKam program (vers. 6.0) and detection histories were created using R (R Core Team, 2020) and the 'camtrap R' package (Niedballa *et al*., 2016). Nominally independent encounters of each species were defined as successive photographs >30 minutes apart, or non-consecutive photographs of the same species at the same station (MacKenzie & Royle, 2005; Chutipong *et al*., 2014; Pin *et al*., 2018). We used 24 hours (starting at 00:00:01 and ending at 23:59:59) as an occasion (one day), yielding 88 occasions in total.

We did not re-analyse the survey data collected in 2009, but instead compared our results to Gray *et al*. (2010). We calculated the camera-trap encounter rate for each species based on their number of independent events, divided by total trap nights and multiplied by 100. Although analysis of simulated data has suggested that encounter rate has limitations when compared to actual densities (Sollmann *et al*., 2013), we feel that this method was adequate for our purpose of comparing the encounter rate of species over time at the same site (Clements *et al*., 2021). We calculated naïve occupancy based on the number of camera stations each species was detected, divided by the total number of stations (MacKenzie *et al*., 2017).

Activity patterns were examined for each species using the R package 'overlap' v.0.3.2 (Meredith & Ridout, 2018). We estimated coefficients of overlapping kernel densities based on times of observations between the large Indian civet and large-spotted civet, the large Indian civet and small Indian civet, and the large-spotted civet and small Indian civet. We also compared the overlap values between species in our study and those in Gray *et al*. (2010) to determine if these changed over time among the civet species. For the comparison between study periods, we used Dhat1 for the estimated coefficients because this is recommended for small sample sizes.

We modelled single-season single-species occupancy (MacKenzie *et al*., 2002) in a Bayesian approach for our target species using the 'wiqid' package (Quick and Dirty Estimates for Wildlife Population) (Meredith, 2015). Two environmental covariates (i.e., distance to water and habitat type) were used as site covariates in the model (MacKenzie & Royle, 2005) and we kept the detection probability constant. We used ArcGIS to define forest cover types at each camera trap station (with a 1 km radius around each camera station) and we calculated the distance from each camera station to streams (km). The forest type layer was produced by WWF Cambodia. We ran three models including constant (null) denoted by [psi(.),p(.)], distance to water denoted by [psi(DWater).p(.)], and forest cover type denoted by [psi(habit).p(.)].

For the Bayesian approach, we ran three chains of Markov Monte Carlo (MCMC) simulations of 100,000 iterations each, discarded 15,000 as initial burn-in, and thinned by one. We compared candidate models using

Watanabe-Akaike information criterion (WAIC) scores (Vehtari *et al*., 2015, 2016; Hollenbach *et al*., 2020). Model convergence was based on the Gelman-Rubin statistic for each parameter, where models successfully converged with a Rhat value <1.1 (Penjor *et al*., 2019; Pin *et al*., 2022). We report posterior means with standard deviations and 95% highest density credible intervals (Penjor *et al*., 2018, 2019; Pin *et al*., 2022). All data analyses were performed in R (R Core Team, 2020).

Results

Our 2019 survey generated 4,402 camera trap days and 129,069 photographs. The encounter rate was lowest for large-spotted civets, whereas it was over four times higher for large Indian civets and almost four times higher for small Indian civets (Table 1). Naïve occupancy was similarly lowest for large-spotted civets, whereas it was over six times higher for large Indian civets and small Indian civets (Table 1). In contrast, during the 2009–2010 survey, the encounter rate and naïve occupancy were higher for large spotted civets than the other two species (Table 1). Between 2009–2010 and 2019, the encounter rate for large-spotted civets decreased by 26% and naïve occupancy decreased by 65% (Table 1). In contrast, the encounter rate and naïve occupancy for large Indian civets increased about threefold from 2009–2010 to 2019 (Table 1). Similarly, the encounter rate for small Indian civets increased twelve-fold and naïve occupancy increased four-fold (Table 1).

For large-spotted civets and large Indian civets, our null model exhibited the lowest WAIC, followed by the model incorporating forest cover type as a site covariate (Table 2). Conversely, the model incorporating distance to water as a site covariate achieved the lowest WAIC score for small Indian civets. For all three civet species, differences in WAIC scores were less than 10, indicating that the null model was preferred (Hollenbach *et al*., 2020). The estimated coefficients of all models for each species are shown in Table 3. For the null model, the estimated detection probabilities for all species were relatively small (less than 0.1) (Fig. 3). The estimated

Table 1 Encounter rate (nominally independent encounters/trap days x 100), number of nominally independent encounters, number of camera locations where each species was recorded, and naïve occupancy (number of camera locations where species was recorded/total number of camera locations) for ground-dwelling civets in Srepok Wildlife Sanctuary, 2019. Camera-trap survey results (Gray *et al*., 2010) from the same site ten years earlier are included for comparative purposes.

Species	Encounter Rate	Nominally Independent Encounters	No. Locations	Naive Occupancy (%)
Present study (n=69 camera stations in 2019)				
Large-spotted civet *Viverra megaspila*	0.73	55	07	10.1
Large Indian civet *Viverra zibetha*	3.28	249	44	63.8
Small Indian civet *Viverricula indica*	2.85	216	43	62.3
Gray *et al*. (2010) (n=69 camera stations in 2009–2010)				
Large-spotted civet	0.99	48	20	29.0
Large Indian civet	0.93	45	15	21.7
Small Indian civet	0.23	13	11	15.9

Species	Models	df	WAIC
Large-spotted civet *Viverra megaspila*	psi (.), p(.)	2	273.795
	psi (habit), p(.)	3	275.564
	psi (DWater), p(.)	3	275.764
Large Indian civet *Viverra zibetha*	psi (.), p(.)	2	1244.971
	psi (habit), p(.)	3	1245.477
	psi (DWater), p(.)	3	1247.188
Small Indian civet *Viverricula indica*	psi (DWater), p(.)	3	1278.583
	psi (.), p(.)	2	1279.519
	psi (habit), p(.)	3	1281.328

Table 2 (Left) Occupancy models for three ground-dwelling civet species, including the number of parameters (df) and the Watanabe-Akaike information criterion (WAIC). DWater = distance to water; habit = forest cover.

Table 3 Estimated coefficients for occupancy modeling of three ground-dwelling civet species provided using Bayesian inference, including posterior means, standard deviations (SD), 95% highest density credible intervals, Rhat values and Monte Carlo standard errors (MCEpc).

Parameters	Mean	SD	Lower 95	Upper 95	Rhat	MCEpc
Large-spotted civet *Viverra megaspila*						
psi(.), p(.)						
psi(Intercept)	-1.217	0.202	-1.618	-0.824	1.000	0.742
p(Intercept)	-1.362	0.094	-1.548	-1.177	1.001	0.750
psi(habit), p(.)						
psi(DDF)	-1.151	0.221	-1.585	-0.718	1.000	0.722
psi(SE)	-1.266	0.421	-2.098	-0.457	1.000	0.746
p(Intercept)	-1.364	0.096	-1.551	-1.176	1.000	0.794
psi(Dwater), p(.)						
psi(Intercept)	-1.238	0.206	-1.647	-0.841	1.000	0.711
psi(DWater)	-0.134	0.214	-0.563	0.277	1.000	0.737
p(Intercept)	-1.363	0.096	-1.555	-1.180	1.000	0.754
Large Indian civet *Viverra zibetha*						
psi(.), p(.)						
psi(Intercept)	0.457	0.170	0.128	0.793	1.000	0.527
p(Intercept)	-1.508	0.042	-1.588	-1.426	1.000	0.829
psi(habit), p(.)						
psi(DDF)	0.575	0.203	0.178	0.974	1.000	0.648
psi(SE)	0.111	0.318	-1.516	0.730	1.000	0.503
p(Intercept)	-1.510	0.042	-1.593	-1.430	1.001	0.849
psi(Dwater), p(.)						
psi(Intercept)	0.462	0.171	0.129	0.798	1.000	0.569
psi(Dwater)	0.023	0.169	-0.352	0.352	1.001	0.530
p(Intercept)	-1.509	0.041	-1.427	-1.427	1.000	0.834
Small Indian civet *Viverricula indica*						
psi(Dwater), p(.)						
psi(Intercept)	0.510	0.191	0.136	0.887	1.000	0.691
psi(DWater)	-0.320	0.187	-0.687	0.047	1.000	0.667
p(Intercept)	-1.523	0.041	-1.603	-1.442	0.999	0.892
psi(.), p(.)						
psi(Intercept)	0.451	0.173	0.108	0.790	1.000	0.589
p(Intercept)	-1.517	0.041	-1.597	-1.438	1.001	0.811
psi(habit), p(.)						
psi(DDF)	0.394	0.199	0.006	0.788	1.000	0.610
psi(SE)	0.578	0.330	-0.073	1.218	1.000	0.514
p(Intercept)	-1.516	0.041	-1.595	-1.435	1.000	0.856

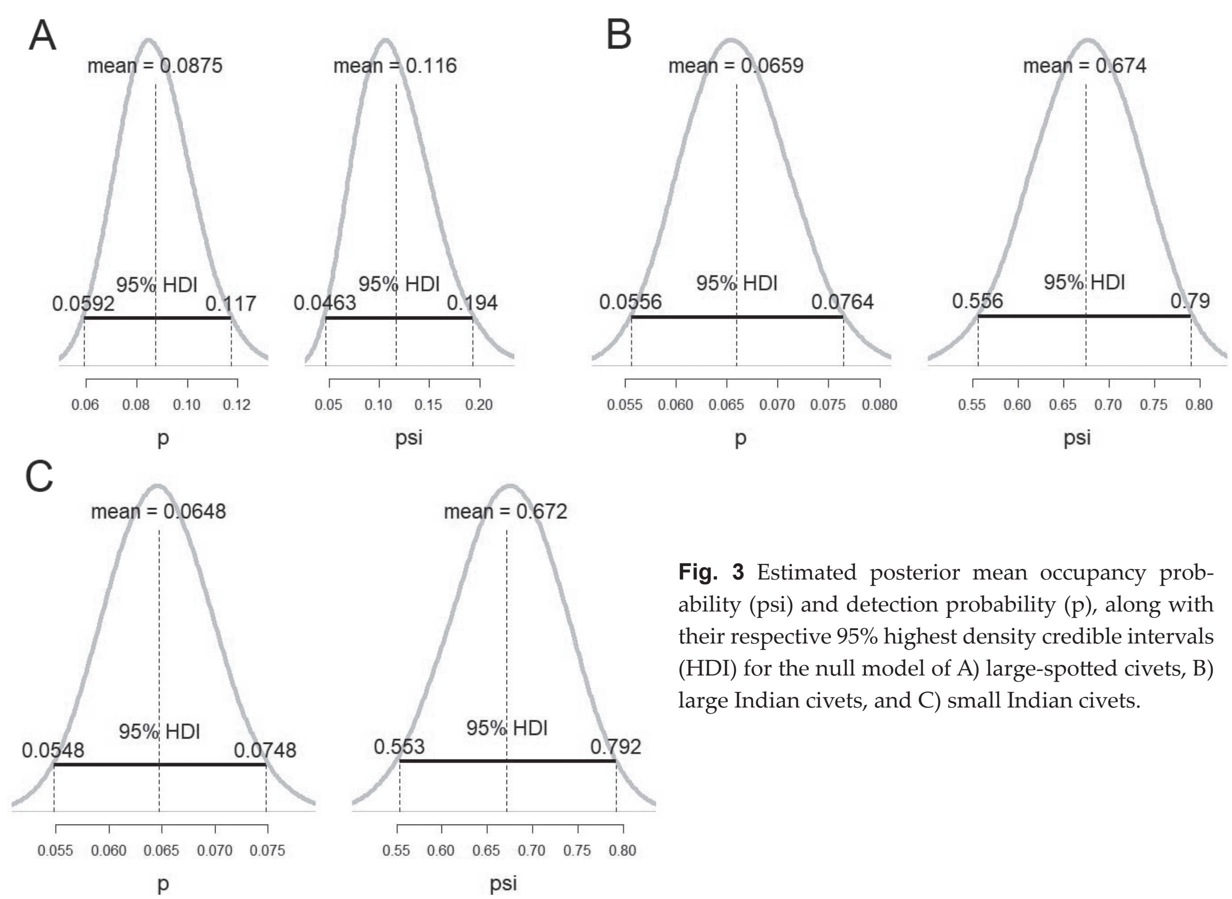

Fig. 3 Estimated posterior mean occupancy probability (psi) and detection probability (p), along with their respective 95% highest density credible intervals (HDI) for the null model of A) large-spotted civets, B) large Indian civets, and C) small Indian civets.

occupancy probabilities for large Indian civets and small Indian civets were similar (both 0.67) and significantly higher than those for large-spotted civets (Fig. 3).

The DDF-dominated lowland areas of SWS had a positive relationship with the occupancy probability of large and small Indian civets and a negative relationship with large-spotted civets (Table 3). The SEF that dominated higher areas of SWS had no effect on the occupancy of large and small Indian civets and a negative relationship with large-spotted civets. Large-spotted civets showed similar occupancy probabilities in DDF (mean = 0.131, CI = 0.047–0.220) and SEF (mean = 0.121, CI = 0.003–0.273). The estimated occupancy probability of large Indian civets was 0.713 (CI = 0.579–0.841) in DDF and 0.542 (CI = 0.309–0.773) in SEF, whereas the small Indian civets had comparable occupancy probabilities in DDF (mean = 0.650, CI = 0.510–0.791) and SEF (mean = 0.708, CI = 0.500–0.909). Distance to water (i.e., rivers) did not significantly affect the occupancy probability of any civet species (Table 3).

All three civet species had similar activity patterns, being almost exclusively nocturnal (Fig. 4). The highest activity peaks for large and small Indian civets occurred just before dawn, whereas large-spotted civets had two peaks in activity, just before dawn and just after sunset (Fig. 4). Estimated coefficients of overlapping kernel densities were 0.752 between large Indian civets and large-spotted civets, 0.898 between large Indian civet and small Indian civets and 0.791 between large-spotted civets and small Indian civets. Overall, activity patterns for each civet species in 2019 were similar to those in 2009–2010 (Gray *et al.*, 2010), indicating these had changed little if any between the two periods (Table 4).

Discussion

Our results show that drastic changes have apparently occurred within the terrestrial civet community in SWS from 2009–2010 to 2019. Although encounter rates were highest for large Indian civets and small Indian civets

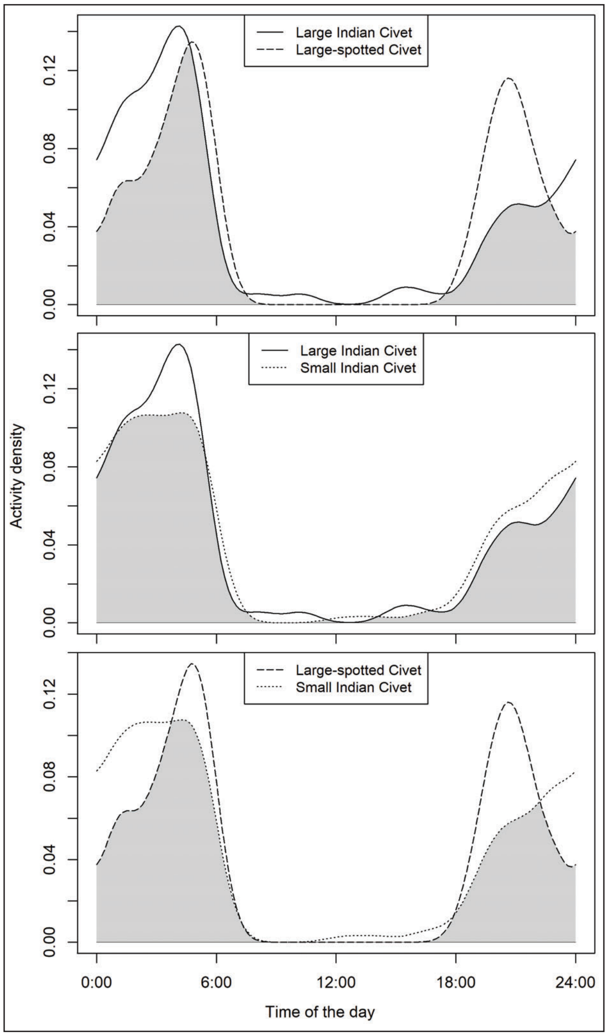

Fig. 4 Comparative activity of large-spotted civets *Viverra megaspila*, large Indian civets *V. zibetha* and small Indian civets *Viverricula indica* in Srepok Wildlife Sanctuary, 2019. Shaded areas represent the coefficient of overlap.

Table 4 Activity overlap based on the estimated coefficients (Dhat1) of overlapping kernel densities between three ground-dwelling civet species in Srepok Wildlife Sanctuary.

Species Overlap	Dhat1	
	2009	2019
Large Indian civet vs. large-spotted civet	0.8157275	0.7529812
Large Indian civet vs. small Indian civet	0.8081864	0.8988771
Large-spotted civet vs. small Indian civet	0.8738956	0.7914684

in 2019, they were highest for large-spotted civets in 2009–2010. Between the two periods, naïve occupancy increased substantially for large Indian civets and small Indian civets, but decreased substantially for large-spotted civets. Following ten years of increased illegal logging when snaring also increased exponentially in SWS (Groenenberg *et al*., 2020), the encounter rate and distribution of large-spotted civets decreased considerably, becoming the least-recorded terrestrial civet in the core zone of SWS based on camera-trap data. Encounter rates and recorded distributions of large Indian civets and small Indian civets increased severalfold in SWS, possibly because these species use a wider altitudinal range and variety of terrain than large-spotted civets. Consequently, the former species could have multiple source populations in the landscape and appear to have flourished in the face of increasing anthropogenic pressures in SWS. We note that encounter rates between studies should be viewed with caution as they might not reflect actual differences in numbers. This is because they could be influenced by other factors such as the use of different camera-trap models, set-up techniques, surveys in different seasons or criteria for station locations. That said, large-spotted and large Indian civets are similar in size and shape, thus differences in camera-trap models should not have affected the detection of these species differently. Additionally, the survey designs were similar between studies and the camera stations in 2019 were actually placed along the same roads and trials as in 2009–2010. Although some camera trapping was conducted during the wet season in the earlier study, most data from that study came from the dry season, so seasonal differences between studies should have been minimal. We therefore conclude that differences in encounter rates between the two studies was influenced most by population changes between the study periods.

Our findings for large and small Indian civets are consistent with studies in other parts of their distributions. Large Indian civets are reported to tolerate considerable habitat modification, and habitat loss and fragmentation are not sufficient to drive population declines (Timmins *et al*., 2016a). The species also appears to be more resilient than large-spotted civets to poaching and indiscriminate snaring (Timmins *et al*., 2016a). In the Nakai-Nam Theun National Protected Area in Laos for example, where intensive market-driven snaring has increased over several decades, large Indian civets were the third most frequently recorded and widespread carnivore (Coudrat *et al*., 2014). In Vietnam, where widespread indiscriminate snaring has led to a decline in most terrestrial mammalian fauna including most small felids, large Indian civets were found in almost half of 13 camera-trapped surveys across the country, albeit in very low numbers (Wilcox *et al*., 2014). This habitat plasticity and relatively greater resilience to poaching therefore seems likely to explain the dramatic increase in encounter rate and recorded distribution for the species in SWS from 2009–2010 to 2019, a time when populations of larger mammal species were devastated in SWS (Groenenberg *et al*., 2020; Rostro-García *et al*., 2023). Additionally, the decrease in large carnivores, some of which consume civets in SWS (Rostro-García *et al*., 2018; Kamler *et al*., 2020), could have also benefited large Indian civets.

Small Indian civets exhibit wide use of and in some cases a preference for degraded and fragmented natural habitats. The species has many healthy populations in agricultural and secondary forest landscapes (Choudhury *et al*., 2015) and can be more common near protected area edges with more disturbed habitats compared to undisturbed forests within protected areas (Johnson *et al*., 2009). It is considered an open forest and edge species and thus has probably benefited from extensive degradation and fragmentation of evergreen forests throughout Southeast Asia (Choudhury *et al*., 2015). The species is also known to persist in the face of heavy hunting that devastates other small terrestrial carnivore populations (Choudhury *et al*., 2015). These attributes probably contributed to the twelve-fold increase in encounter rates for small Indian civets from 2009–2010 to 2019, despite increased poaching and illegal logging in SWS.

Large-spotted civets have much narrower habitat requirements, as the species is typically restricted to elevations <300 m and areas of gentle terrain (Timmins *et al*., 2016b). It also appears to affected more by human hunting than the other two terrestrial civets (Timmins *et al*., 2016b), although it is not clear why indiscriminate snaring (the most common type of poaching in SWS) would negatively affect this species more. It could be the large-spotted civets have a lower intrinsic growth rate (e.g., smaller litters, less frequent births, etc), allowing their populations to be more negatively impacted by mortalities caused by poaching. Regardless of the reasons, our results suggest that a major decline has occurred in large-spotted civet populations in SWS over a ten-year period. This does not bode well for the future of the species in the landscape and these findings have global implications because eastern Cambodia has been considered a stronghold for the species.

Our occupancy modelling showed that large and small Indian civets were positively associated with DDF, whereas the reverse was true for large-spotted civets, suggesting some level of habitat partitioning among the civet species. This is surprising given previous research in SWS showed that large-spotted civets preferred DDF, whereas the large Indian civet was more of a habitat generalist (Gray *et al*., 2010). Our findings are more similar to those made in the northern plains of Cambodia (Suzuki *et al*., 2017) and other parts of their range (Timmins *et al*., 2016b), where large-spotted civets were found in all forest types, albeit at low elevations. Nearly all illegal logging and snaring within SWS is within SEF patches with much less in DDF, so perhaps the small and large Indian civets used more DDF because it was less affected by logging and other human activities. Because long-term data are essential for accurately assessing population density trends, we recommend future camera-trap surveys with similar efforts for civets to monitor their population changes and habitat use in SWS. Future research should also focus on investigating the mechanisms facilitating coexistence within the civet community, particularly exploring the existence of a dominance hierarchy among the species.

Our results suggest the activity patterns of all three civet species are similar and almost completely nocturnal, indicating no temporal partitioning between them. These results are consistent with those in 2009–2010 (Gray *et al*., 2010) and suggest that a decade of increasing human activities within SWS have not affected the activity patterns of the civet community. Because illegal human activity within SWS is primarily diurnal (Rostro-García *et al*., 2023), it presumably did not affect the activities patterns of the nocturnal civet species.

Conservation implications

The Endangered large-spotted civet is experiencing a decrease in encounter rates and recorded distribution in SWS in eastern Cambodia, which is considered a global stronghold for the species (Gray *et al*., 2010). This decrease is plausibly related to the exponential increase in snaring and illegal logging that has occurred in the EPL over the last decade, devastating large mammal populations (Groenenberg *et al*., 2020; Rostro-García *et al*., 2023). In contrast, ground-dwelling small carnivores not confined to level terrain in lowland areas are persisting and even apparently increasing in the face of poaching and habitat-induced changes to the landscape, as evidenced by large and small Indian civets. Unfortunately, indiscriminate snaring is still increasing in SWS and other areas within the EPL (Rostro-García *et al*., 2023) and illegal logging and other forms of habitat loss are expected to continue. Unless a concerted effort is made to reduce poaching and habitat loss in the EPL, which would be a massive task, large-spotted civets may follow tigers, leopards and other larger carnivores in the EPL in becoming extinct in one of its last strongholds in the near future (O'Kelly *et al*., 2012; Rostro-García *et al*., 2023). To protect remaining wildlife in the EPL, especially globally threatened species, immediate actions such as strengthening law enforcement, intensifying anti-poaching efforts and engaging local communities to reduce poaching pressure are crucial. These will require coordinated efforts from government agencies, NGOs, and local communities, which are difficult to implement but necessary for successful wildlife conservation in eastern Cambodia.

Acknowledgements

We thank WWF-Cambodia and the Wildlife Conservation Research Unit, University of Oxford, for supporting our camera trap survey. We also thank Dr HE Say Samal (former Minister of Environment), HE Kim Nong (former Directorate of the General Department for Natural Protected Area [GDNPA]) and Mr. Chou Sophark (former director of the Eastern Mekong Terrestrial Protected Area Conservation Department) for permission to carry out the fieldwork in SWS. Finally, we thank the field teams, including rangers from SWS, for their help with conducting the surveys.

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