Global Ecology and Conservation 20 (2019) e00766

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Original Research Article

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

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A R T I C L E I N F O

Article history:
Received 15 April 2019
Received in revised form 24 August 2019
Accepted 24 August 2019

Keywords:
Clouded leopard
Dhole
Dynamic multispecies occupancy model
Laos
Nam Et - Phou Louey National Protected Area
Tiger

A B S T R A C T

The Nam Et - Phou Louey National Protected Area (NEPL) is known for its diverse community of carnivores, and a decade ago was identified as an important source site for tiger conservation in Southeast Asia. However, there are reasons for concern that the status of this high priority diverse community has deteriorated, making the need for updated information urgent. This study assesses the current diversity of mammals and birds in NEPL, based on camera trap surveys from 2013 to 2017, facilitating an assessment of protected area management to date. We implemented a dynamic multispecies occupancy model fit in a Bayesian framework to reveal community and species occupancy and diversity. We detected 43 different mammal and bird species, but failed to detect leopard *Panthera pardus* and only detected two individual tigers *Panthera tigris*, both in 2013, suggesting that both large felids are now extirpated from NEPL, and presumably also more widely throughout Lao PDR. Mainland clouded leopard *Neofelis nebulosa* had the highest estimates of probability of initial occupancy, persistence and colonization, and appeared to be the most widely distributed large carnivore, followed by dhole *Cuon alpinus*. Both of these species emerge as a priority for further monitoring and conservation in the NEPL landscape. This study provides the most recent assessment of animal diversity and status in the NEPL. Our analytical approach provides a robust and flexible framework to include sparse and inconsistent data sets of multiple species to assess their status via occupancy as a state process, which can often provide insights into population dynamics.

1. Introduction

The Nam Et - Phou Louey National Protected Area (hereafter NEPL) in northern Lao PDR (hereafter Laos) is known for its high biodiversity including a rich carnivore community (Johnson et al., 2006). A decade ago NEPL was considered home to one of the most important tiger populations in all of Laos, Cambodia, and Vietnam, and an important source site for tiger conservation in Southeast Asia (Walston et al., 2010). However, the current situation is unknown, and there is widespread

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https://doi.org/10.1016/j.gecco.2019.e00766

concern that poaching may be reaching unsustainable levels (Gray et al., 2017b). Surveys in the 1990s suggested that NEPL has been found to hold most of the species of bird and large mammal that would be expected on biogeographic and habitat grounds, comprising 6 felid species, dhole, *Cuon alpinus*, 2 bear species, Asian elephant, *Elephas maximus*, 14 other small carnivore species, 7 ungulate species, 5 primate species, and 299 bird species (Johnson, 2012). The first systematic camera trap surveys were conducted during 2003–2004 to determine the baseline of large carnivore and prey species (Johnson et al., 2006) together with subsequent surveys up until 2008 confirmed the presence of the aforementioned carnivore, ungulate, primate and some smaller mammal species. Unregulated over-harvesting of animals and plants as well as loss of forest to agricultural expansion are the main threats to wildlife of the NEPL (Johnson, 2012). The study by Johnson et al. (2016) suggested a decline in abundance of tiger (*Panthera tigris*) and an increase in the abundance of some large ungulate prey over a period of seven years (2005–2012) during the implementation of a new law enforcement strategy. In this study, we add more recent data from the largest camera trapping effort ever conducted in Laos and assess the most recent status of the carnivores and prey species based on three surveys in four blocks undertaken between 2013 and 2017. We thereby assess the outcome of protected area management and provide a new baseline for future wildlife management planning and action in the NEPL.

Of all the biodiversity in NEPL, this site has earlier been recognized as globally important for conserving breeding populations of the Endangered tiger (Johnson, 2012), and Endangered dhole (Kamler et al., 2012). In fact, NEPL was thought to harbour the last breeding population of tigers in Indochina (Johnson et al., 2016), and was identified as one of the most important source sites for tiger conservation in Southeast Asia (Walston et al., 2010). Additionally, based on 2000s surveys, it was hoped that NEPL would retain a leopard population, which have dramatically declined throughout all of Southeast Asia (Rostro-García et al., 2016). Management and enforcement policies in NEPL during the past 10 years have focused on conserving the tiger, but it is unclear whether these interventions have succeeded in conserving these globally important populations of tigers, leopards, and dholes.

According to Peet (1974), diversity has two components: (i) species richness (the number of species that live in a specific area); and (ii) species evenness (or relative degrees of commonness and rarity of the species in the community). Although species richness is very widely used as a measure of biological diversity, it alone does not indicate the health of an ecosystem because diversity indices can remain high despite the extinction of some rare species (Travaini et al., 1997). Therefore, auditing the status of an area's diversity necessitates knowledge of both species' abundance (e.g., occupancy as a proxy) and richness. We infer the relative degree of species commonness through hierarchical multispecies occupancy models, which allow us to estimate and model occupancy at both individual and communities levels, while accounting for species-specific detection probabilities (Kéry and Royle, 2016). It also enables us to evaluate changes in species composition and occupancy in multiple areas over time (Tobler et al., 2015).

2. Materials and methods

2.1. Study area

The NEPL is the largest protected area in Laos, covering 5969 km^2 of mountainous terrain across seven districts and three provinces (Houaphan, Luang Prabang, and Xiengkhuang). It is located in the northern highlands of Laos (between latitude 19°50' - 20°50′N and longitude 103°00' - 103°53′E), bordering Vietnam along its northern boundary (Fig. 1). NEPL has an elevation ranging from 400 to 2257 m and is largely dominated by dry evergreen and semi-evergreen forests (Johnson, 2012). However, around one third of the park is degraded forest with a canopy cover of less than 20%. The area has a tropical monsoonal climate with a rainy season lasting from May to October (with annual rainfall of 1400–1800 mm), followed by a distinct dry season for the remainder of the year (Johnson, 2012).

The NEPL is divided into a totally protected core zone where human activity is prohibited, and a managed use zone where specified livelihood activities are permitted following NPA regulations (Johnson, 2012, Fig. 1). There are approximately 34 villages in the management zone, with some of these being just inside the core zone (Johnson, 2012). The livelihood of the villagers include legal activities (e.g., gathering non-timber forest products, shifting cultivation, livestock raising, and subsistence hunting using traditional methods) and some illegal activities (e.g., hunting for trade using modern guns and snares), all of which undoubtedly puts stress on the wildlife populations of NEPL.

2.2. Data collection

Systematic camera trap surveys were carried out within the NEPL core zone from 2013 to 2017 in four blocks of ~200 km^2. The Nam Poung - Na Vaen (NV) area (Fig. 1) is mainly dominated by semi-evergreen and evergreen forest. This block almost completely covered the sampling Block 1 of the previous surveys between 2003 and 2004 (Johnson et al., 2006). The Pha Daeng (PD) area is mainly dominated by semi-evergreen and grassland and covered 80% of the sampling Block 3 of the previous survey (Fig. 1). The Phoupha - Siphou (PS) area is dominated by semi-evergreen forest with a small mixture of evergreen forest and patches of grassland. The Nam Neun (NN) area is defined by low density semi-evergreen forest with patches of high density semi-evergreen forest and shrub/bamboo forest. This is the smallest block, measuring 145 km^2 and overlapping Sampling Block 2 of the previous survey by about 50% (Fig. 1).

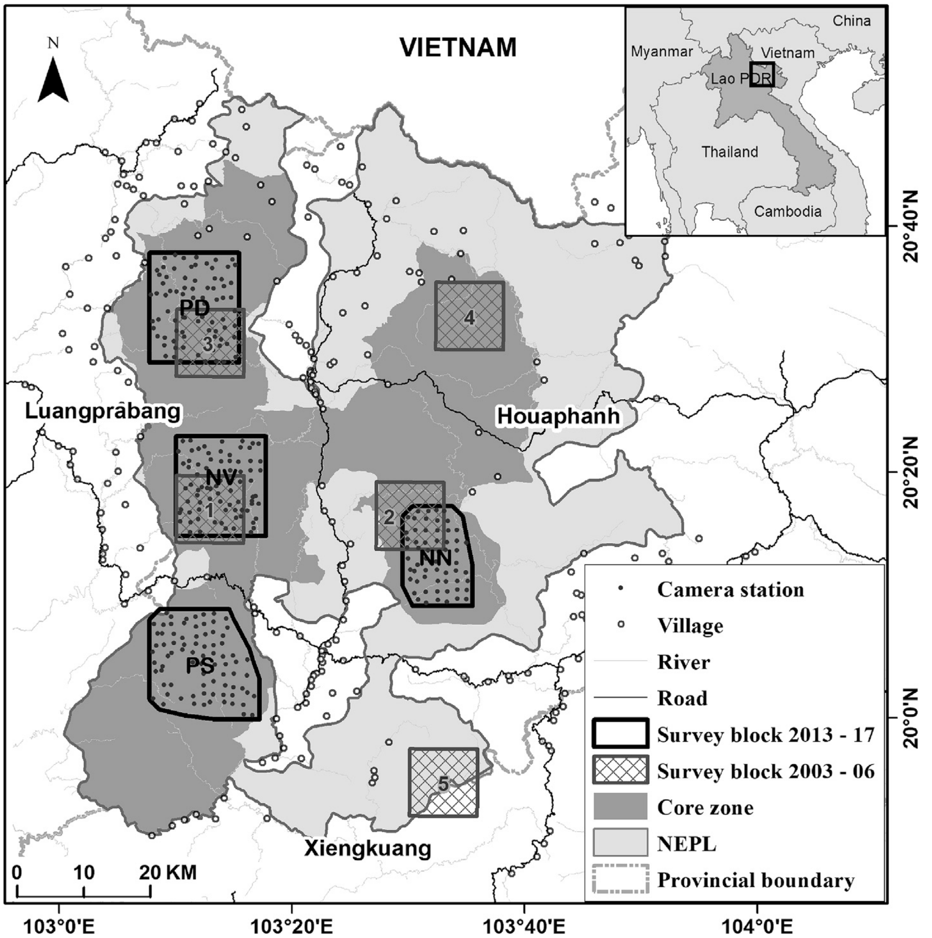

Fig. 1. The Nam Et - Phou Louey National Protected Area (NEPL), Laos, with 2013–2017 survey blocks (NV = Nam Poung - Na Vaen; PD = Pha Daeng; PS = Phoupha - Siphou; and NN = Nam Neun) and the 2003–2006 survey blocks (numbered from 1 to 5).

For NV, PD and PS blocks, camera traps were set in pairs at 80 locations at 1–1.5 km spacing between locations. The surveys were repeated three times (Table 1). We used a mixture of infrared camera trap models: CuddeBack Ambush IR – Model 1187, Reconyx Hyperfire HC500, and MAGINON–WK 3 HD camera traps. The NN block contained 60 camera trap sites and was surveyed in only one year because of funding limitations (Table 1).

Traps were located at between 629 and 2185 m altitude: 16% were below 1000 m, 16% between 1000 and 1500 m, and 68% above 1500 m. About 63% of the sites were in closed forest – evergreen and high density semi-evergreen forests. The camera traps were placed mostly along ridgelines and animal trails, and at points where trails meet streams. Each camera was set without baits at 35 cm above the ground and was set to work throughout the 24-hr cycle. Although cameras used by Johnson et al. (2006) were set at 45 cm above the ground, we do not think this difference would significantly affect animal detections between studies because small, medium and large species would presumably trigger cameras at the same rate when set at both 35 and 45 cm. This is because trigger mechanisms have a cone-shaped field of view leading out from each camera, and therefore would have a similar field of view when set 2–3 m from the trail. Each survey period lasted for a minimum of 49 days.

2.3. Data organisation and preparation

Each camera-trap photo of an animal was identified, and organised using the CamtrapR (Niedballa et al., 2016). Notionally independent events, following O'brien et al. (2003), were used for our analysis. We included records from a total of 43 species including: large to small-sized carnivores, ungulates, primates, birds and rodents (Table 2). The species were also grouped based on their primary diet guilds which are carnivore, herbivore, insectivore and omnivore. To reduce heterogeneity and reduce the computational burden of model fitting, we aggregated our data into 10-day sampling occasions; there were a total of five occasions per year.

Table 1
Camera trap survey dates, effort and altitude in four blocks in Nam Et - Phou Louey National Protected Area, Laos, during 2013–2017.

Block, site name	Survey name	Date	Duration (days)	Station (cameras)	Trap days	Altitude (m)
1, Nam Poung - Na Vaen						
	NPNV1	3-5/2013	53	80 (160)	3831	983–2185
	NPNV2	3-5/2015	52	80 (158)	3200	
	NPNV3	2-4/2017	52	80 (156)	3530	
2, Pha Daeng						
	PD1	11/2013–1/2014	51	80 (159)	3693	709–1739
	PD2	5-7/2015	51	80 (156)	3282	
	PD3	4-5/2017	50	80 (160)	3240	
3, Phoupha - Siphou						
	PS1	2-4/2014	54	80 (160)	3446	629–1514
	PS2	2-4/2016	50	80 (160)	3003	
	PS3	6-8/2017	49	80 (160)	1977	
4, Nam Neun	NN1	5-7/2014	54	60 (120)	2825	720–1522

Table 2
Species recorded during camera trap surveys from 2013 to 2017 in Nam Et - Phou Louey National Protected Area, Laos.

Family	Scientific name	Common name	Status[a]	Sampling block (no. observed stations)			
				NP	PD	PS	NN
Bovidae	*Bos gaurus*	Gaur	VU	1	0	1	0
	Capricornis milneedwardsii	Indochinese serow	NT	58	49	24	3
Canidae	*Cuon alpinus*	Dhole	EN	37	22	20	3
Cercopithecidae	*Macaca assamensis*	Assamese macaque	NT	11	6	7	5
	Macaca leonina	Northern pig-tailed macaque	VU	1	1	5	0
	Macaca mulatta	Rhesus macaque	LC	4	5	4	4
	Macaca arctoides	Stump-tailed macaque	VU	101	104	15	21
Cervidae	*Muntiacus vaginalis*	Northern red muntjac	LC	128	151	98	31
	Cervus unicolor	Sambar	VU	28	9	8	2
	M. rooseveltorum complex	Small dark muntjac(s)	DD	80	63	19	2
Felidae	*Catopuma temminckii*	Asian golden cat	NT	32	42	23	7
	Neofelis nebulosa	Mainland clouded leopard	VU	24	40	33	5
	Prionailurus bengalensis	Leopard cat	LC	33	42	29	3
	Pardofelis marmorata	Marbled cat	VU	32	27	19	2
	Panthera tigris	Tiger	EN	12	2	0	0
Herpestidae	*Herpestes urva*	Crab-eating mongoose	LC	49	19	31	2
Hystricidae	*Atherurus macrourus*	Asian brush-tailed porcupine	LC	18	25	13	1
	Hystrix brachyura	East Asian porcupine	LC	40	37	18	8
Muridae		Rat morphotype 1	LC	2	10	27	0
		Rat morphotype 2	LC	19	15	12	0
		Rat morphotype 3	LC	2	3	0	0
Mustelidae	*Melogale* spp.	Ferret badger(s)	LC	3	5	4	0
	Arctonyx collaris	Greater hog badger	VU	64	41	61	9
	Martes flavigula	Yellow-throated marten	LC	78	79	42	12
Phasianidae	*Polyplectron bicalcaratum*	Grey peacock pheasant	LC	21	25	13	6
	Lophura nycthemera	Silver pheasant	LC	47	42	37	8
	Gallus gallus	Red junglefowl	LC	11	22	8	6
		Unidentified partridge(s)	LC	8	8	11	0
Prionodontidae	*Prionodon pardicolor*	Spotted linsang	LC	11	11	6	0
Sciuridae		Squirrel morphotype 1	LC	3	0	0	0
	Ratufa bicolor	Black giant squirrel	NT	5	1	1	0
	Tamiops complex	Striped squirrel(s)	LC	0	0	2	0
	Callosciurus erythraeus and/or C. inornatus	Pallas's and/or Inornate Squirrel	LC	6	16	1	0
		Squirrel morphotype 2	LC	4	11	14	0
Suidae	*Sus scrofa*	Eurasian wild pig	LC	45	55	34	9
Ursidae	*Ursus thibetanus*	Asian black bear	VU	6	3	0	2
	Helarctos malayanus	Sun bear	VU	50	29	21	4
Viverridae	*Arctictis binturong*	Binturong	VU	6	6	4	0
	Paradoxurus hermaphroditus	Common palm civet	LC	34	28	23	2
	Viverra zibetha	Large Indian civet	LC	41	51	64	2
	Paguma larvata	Masked palm civet	LC	56	42	30	2
	Chrotogale owstoni	Owston's civet	EN	12	3	0	0
	Viverricula indica	Small Indian civet	LC	1	9	5	0

NV = Nam Poung - Na Vaen; PD = Pha Daeng; PS = Phoupha - Siphou; NN = Nam Neun.
[a] Based on IUCN Red List of Threatened Species, LC = Least concern; NT = Near threatened; VU = Vulnerable; EN = Endangered.

2.4. Data analysis

We implemented a dynamic community model (DCM) as described in Kéry and Royle (in prep), also known as a dynamic multispecies occupancy model (Dorazio et al., 2010) in a Bayesian framework. In common with other occupancy models, the main assumptions of a DCM within each primary period are: (i) no extinction and colonization at the stations over replicated secondary periods (but both are allowed between primary periods); (ii) all detected species are correctly identified; and (iii) the detection probability and occupancy at a station are independent of detection and occupancy at another station (Iknayan et al., 2014).

Although our data set is the result of an immense field effort and comprises thousands of photographs, statistically it is still sparse. Hence, we did not employ data augmentation (Kéry and Royle, 2016) in the analysis of our DCM, because it could lead to unrealistically high estimates of species richness (Guillera-Arroita et al., 2019). Hence, species richness estimates will refer to a maximum of 43, which is the list of species observed in our study. The DCM can formally be described in simple stages:

(1) Initial state for species k: $z_{i,1,k} \sim Bernoulli(\Psi_k)$
(2) State dynamics for species k: $z_{i,t+1,k} | z_{i,t,k} \sim Bernoulli(z_{i,t,k}\phi_k + (1 - z_{i,t,k})\Upsilon_k)$
(3) Observation process for species k: $y_{i,t,k} \Big| z_{i,t,k} \sim Binomial(z_{t,k}p_{i,k})$

In this model $z_{i,t,k}$ is the true presence/absence state of species k at camera station i during primary period t and $y_{i,\ t,\ k}$ are the observed data: the detection frequencies, or the sum of sampling occasions out of five annual occasions that the species k was detected at station i in year t. The model has four primary parameters psi (ψ), phi (ϕ), gamma (Υ), and p denote the probability of initial occupancy, persistence, local colonization and detection, respectively. Initial occupancy is the probability that species k is occurring at station i during time period one. Persistence is the probability of station i remaining occupied by species k during period $t + 1$ given that the species was present during the previous period. Colonization is the probability that the station i becomes occupied by species k during period $t + 1$ given that the species was absent during the previous period. Probability of detection is the probability of detecting species k at station i given that the species is actually present.

We accounted for heterogeneity between 43 recorded species by fitting separate parameters for each species and treating these parameters as random effects, with hyperparameters that are estimated from the data and which formally describe the entire community of the 43 species detected during our study. Thus, in our model we created a link between the parameters of each species and the parameters that describe the community by assuming that the species-level parameters (on the logit scale) were draws from a Normal distribution,

$$\theta_k \sim Normal\left(\mu_\theta, \sigma_\theta^2\right)$$

where θ stands for any of the four primary parameters in the model. The parameters of the Normal distribution describe the community from which the 43 study species are assumed to be sampled from, such that μ_θ is the community average for θ (it could also be thought of as the value for the average species) and σ_θ^2 is the variance among species in that parameter. Thus, the mean hyperparameter describes the central tendency of the parameter values among all species in the community, while the variance hyperparameter describes the heterogeneity among species in that parameter.

In addition, we had to account for possible non-independence of parameters owing to the clustering of camera trap stations in the four blocks b, in which the 300 stations were nested. Due to the fact that the 300 data points are not independent, but instead there is a dependency due to the blocking in our study, we therefore accounted for this by adding random block effects in only initial occupancy and detection. For computational parsimony, for each species, we fitted a single block effect for detection for all years instead of fitting a separate block effect in every year (and for every species). Also, for parsimony, we did not fit block effects in persistence and colonization parameters. We also assumed that guild g (four diet guilds) affected the mean of the parameters for species, but that it does not affect the heterogeneity among species. To account for this assumption, instead of fitting a single Normal distribution for each parameter type (to present species-by-species variability in ψ, φ, Υ or p), as shown above, we estimated four such Normal distributions for each parameter where the mean of the four is different, but the variance is identical. Therefore, submodels for initial occupancy probability, persistence, colonization and detection can be described as follows (where the modelling is applied on the logit scale, as customary for data such as ours):

The submodel for initial occupancy had the sum of $lpsi1_k$ and $lpsi.block_{block_i,\ k}$ on the logit scale, i.e., a species-specific intercept and species-specific random block effect. Both are assumed to be drawn from two Normal distributions with a mean and standard deviation hyperparameters.

$$logit(\psi_{i,k}) = lpsi1_k + lpsi.block_{block_i,\ k}$$

$$lpsi1_k \sim Normal\left(mu.lpsi1_{guild_k},\ sig.lpsi1\right)$$

$$lpsi1.block_{b,k} \sim Normal(0,\ \ sig.lpsi1.block_k)$$

The submodels for persistence and colonization were similar but lacked a block effect (for computational reasons in our relatively sparse data set).

For persistence:

$$logit(\phi_{i,k}) = lphi_k$$

$$lphi_k \sim Normal\left(mu.lphi_{guild_k},\ \ sig.lphi\right)$$

For colonisation:

$$logit(\gamma_{i,k}) = lgamma_k$$

$$lgamma_k \sim Normal\left(mu.lgamma_{guild_k},\ \ sig.lgamma\right)$$

Finally, the submodel for detection was analogous to that for initial occupancy:

$$logit\left(p_{i,k}\right) = lp_k + lp.block_{block_i,\ \ k}$$

$$lp_k \sim Normal\left(mu.lp_{guild_k},\ \ sig.lp\right)$$

$$lp.block_{b,k} \sim Normal(0,\ \ sig.lp.block_k)$$

Estimates of species richness were derived from the posterior distribution of z, i.e., the presence/absence indicators for every species, site and year. The posterior distributions of our model parameters were estimated using Markov Chain Monte Carlo implemented in JAGS (version 4.2.0) through program R (jagsUI; Kellner, 2015). The model was run for 3 parallel chains with 100,000 values retained per chain after discarding 50,000 for adaptation and burn-in and thinning by 10. The Gelman-Rubin statistic was used to assess model convergence, where value < 1.1 denotes convergence (Gelman and Rubin, 1992). Based on Gelman-Rubin diagnostics, there was no evidence of the lack of convergence for the model. We also calculated the Bayesian *p-value* and "lack-of-fit" of the model to assess model fit based on the Freeman-Tukey statistic (Freeman and Tukey, 1950). The estimated Bayesian *p-value* and the lack-of-fit were 1 and 1.13, respectively. The lack-of-fit is directly the analogous quantity to what is often called c-hat in capture-recapture. That is, the variances of the estimates would have to be multiplied by that value, which is equivalent to multiplying the SEs by sqrt (c.hat). In our case, this would make the SEs longer by just 6% (i.e., sqrt (1.13) = 1.063015). Therefore, this slight degree of lack-of-fit was ignored, since we think it is inconsequential for our inferences.

3. Results

3.1. Raw data summaries

Over the 32,027 trap nights of our total survey effort, in total 9762 notionally independent encounters of wildlife were recorded (Table 1). From these records, 43 different species were detected (Table 2). These include 5 species of cats, dhole, 2 species of bear, 11 species of small carnivores (mustelids, civets, mongooses and spotted linsang), 6 ungulate species, 4 species of macaques, and 14 other prey species (small mammals and birds). Importantly, tiger was detected only in the first year of the surveys (in 2013), but not in later years of our study (Table A.1). The leopard was not detected during our study.

3.2. Species and community inferences using the dynamic community model

The dynamic community model for multispecies provided estimates of predicted detection probability, initial occupancy, rate of persistence and colonization, corrected for imperfect detection, for each of the 43 species. Additionally, the mean estimates of each of these parameters for each of the four diet guilds (i.e., carnivore, herbivore, insectivore and omnivore) were also produced as a result of the model.

3.2.1. Species and dietary guild group initial occupancy, persistence and colonization

The estimated mean of initial occupancy for tiger was 0.20 ± 0.21 Standard Deviation (95% Bayesian credible interval 0.001, 0.71), however, its probability of persistence and colonization estimates were lowest in the carnivore category (Fig. 2a, b, c). Mainland clouded leopard *Neofelis nebulosa* had the highest estimates in probability of initial occupancy, persistence and

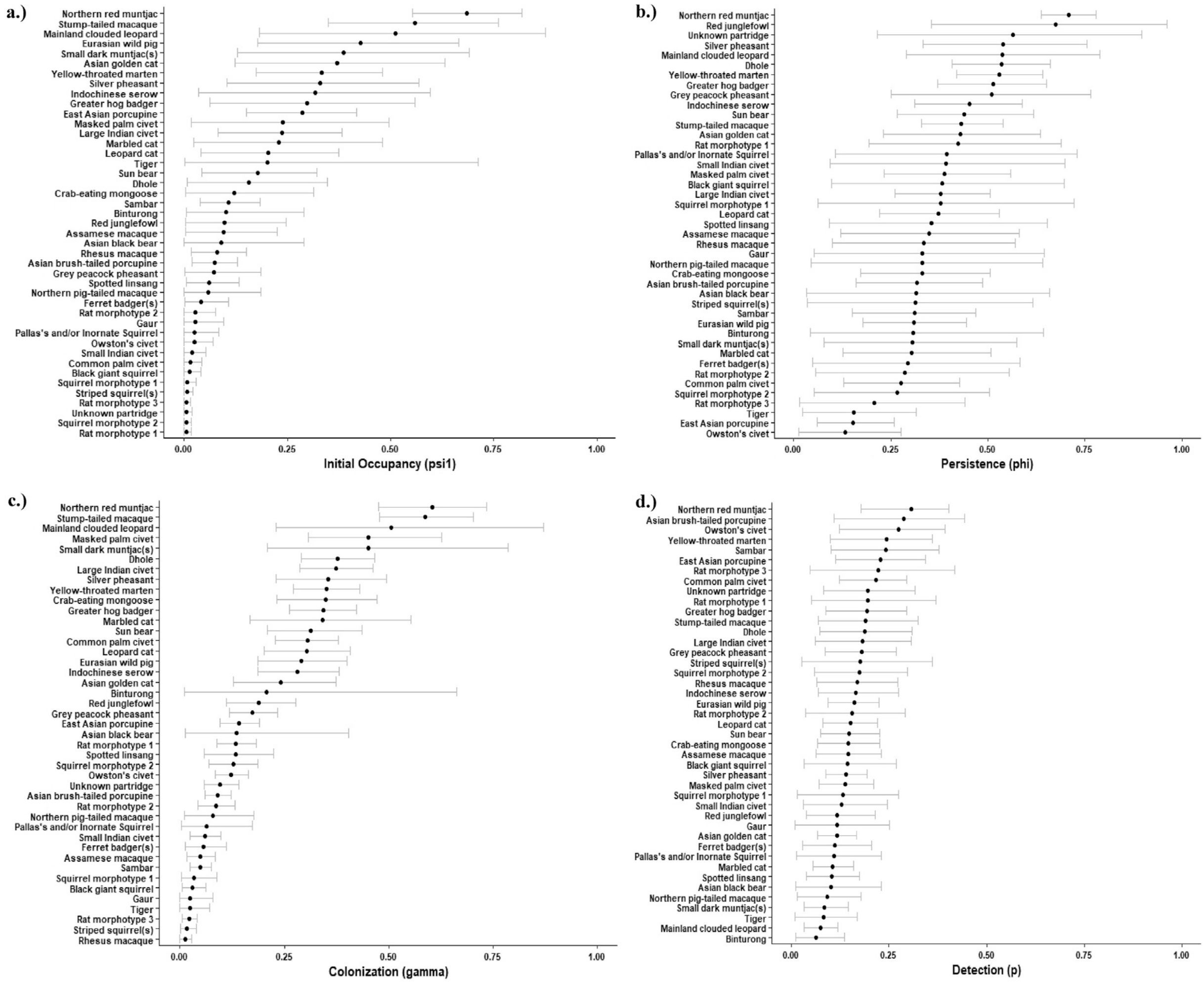

Fig. 2. Bar-plots of estimated mean detectability, occupancy, persistence and colonization of species detected in Nam Et - Phou Louey National Protected Area, Laos, during 2013–2017.

colonization (0.51 ± 0.18 [0.18, 0.88]; 0.54 ± 0.13 [0.29, 0.79]; 0.51 ± 0.17 [0.23, 0.87], respectively), compared with the rest of the carnivore category (Fig. 2a, b, c). Dhole had the second highest in initial occupancy 0.39 ± 0.15 (0.13, 0.69) but its rate of persistence was similar to that of the tiger (Table A.2 and Table A.3). Interestingly, dhole had rate of colonization about 20 times higher than tiger (see Table A.4). Estimated initial occupancy of Asian golden cat *Catopuma temminckii* 0.38 ± 0.13 (0.12, 0.63) was similar to that of the dhole. Although the rate of persistence of the Asian golden cat was slightly higher, its colonization rate was half that of dhole. Surprisingly, the initial occupancy estimates for leopard cat *Prionailurus bengalensis* and marbled cat *Pardofelis marmorata* were almost as low as that of the tiger 0.20 ± 0.09 (0.04, 0.37) and 0.23 ± 0.13 (0.02, 0.48), except that their rates of persistence were twice as high and rates of colonization were 15 times higher than that of the tiger (see Table A.3 and Table A.4).

Among the small, non-felid carnivores, yellow-throated marten *Martes flavigula* had the highest mean initial occupancy and persistence estimates, followed closely by greater hog badger *Arctonyx collaris*, but their rates of colonization were less than those of masked palm civet *Paguma larvata* (Fig. 2a and b). The common palm civet *Paradoxurus hermaphroditus* was shown to have the lowest estimates for initial occupancy and persistence, but its colonization rate however was 30-fold higher than the initial occupancy. Overall, apart from yellow-throated marten and greater hog badger, the estimated means of initial occupancy for other species in this group were still lower than 0.5. None of the small, non-felid carnivores had mean estimates of greater or equal to 0.5 for persistence and colonization (Fig. 2b and c).

Of the two bear species detected during the survey, the estimated means of initial occupancy, persistence and colonization for sun bear *Helarctos malayanus* were higher than the estimates for Asian black bear *Ursus thibetanus* (Fig. 2a, b, c). However, their estimated means of initial occupancy were fairly low and even lower than the mean estimate for the tiger and other cats. Interestingly, the estimated rate of persistence and colonization for both bear species were much higher, compared to the mean estimates for tiger (Fig. 2b, c).

Among the prey species, northern red muntjac *Mutiacus vaginalis* had the highest mean of initial occupancy, persistence and colonization, as the estimates for all three parameters for this species were above 0.6. Stump-tailed macaque *Macaca arctoides* had the second highest estimates, especially for initial occupancy and colonization rates. Eurasian wild pig *Sus scrofa* had the third highest mean estimate of initial occupancy but its rates of persistence and colonization were about 2–3 times lower than those of red muntjac. For the small dark muntjac(s) *M. rooseveltorum* complex, its initial occupancy was about 5 times lower than that of the northern red muntjac, its rate of persistence however is slightly above 0.5 and its colonization rate was slightly higher than that of Eurasian wild pig. Among small mammal prey species, East Asian porcupine *Hystrix brachyuran* had the highest mean estimates of initial occupancy, persistence and colonization. In the insectivore or bird group of prey species, silver pheasant *Lophura nycthemera* had the highest mean estimates of initial occupancy and colonization with the persistence rate of slightly above 0.5 (Fig. 2a, b, c). The model results showed very low estimates of all three parameters for large ungulate species (i.e., gaur *Bos gaurus*, sambar *Cervus unicolor* and Indochinese serow *Capricornis milneedwardsii*) and other small mammals such as squirrels and rats (Fig. 2a, b, c and Table A.2, 3, 4).

At the dietary guild level, carnivores and insectivores had the same initial occupancy rates and were higher than omnivores and herbivores. However, the initial occupancy values of all groups were well below 0.5 (Fig. 3a). In terms of the probability to persist, insectivores were highest among the groups followed by carnivores, and then herbivores and omnivores. There was a very minimal difference among the estimated mean probability of colonization for carnivores, insectivores and omnivores whereas herbivores had the lowest estimated probability. Despite some differences in the probability of colonization, the mean estimates for all groups were considerably low and below 0.3.

3.2.2. Species and dietary guild group detectability

The estimated means of detection probability varied slightly among the species and overall estimates were below 0.5 (Fig. 2d). At the diet guild level, carnivores had the lowest estimated detection probability 0.12 ± 0.02 (0.08, 0.16). While the estimates of detection probabilities for the other three guild groups were slightly higher, the differences among all dietary guilds were seemingly minimal to non-existent (Fig. 3d). Amongst carnivores detected, the yellow-throated marten had the highest detection probability with binturong *Arctictis binturong* having the lowest rate of detection (see Table A.5). There were no differences in the mean detection probability amongst any of the felids or dhole. The general pattern was that small carnivores had higher detection probabilities than large and medium sized-carnivores (Fig. 2d). Amongst the large and medium-sized prey species, red muntjac, Asian brush-tailed porcupine *Atherurus macrourus*, sambar, and East Asian porcupine had the highest estimated detection probability (see Table A.5).

3.3. Species richness

The number of species estimated to occur each year varied little. Of 43 species examined here, 39 species were estimated to occur during the first year and 43 were estimated for the subsequent years (Table 3).

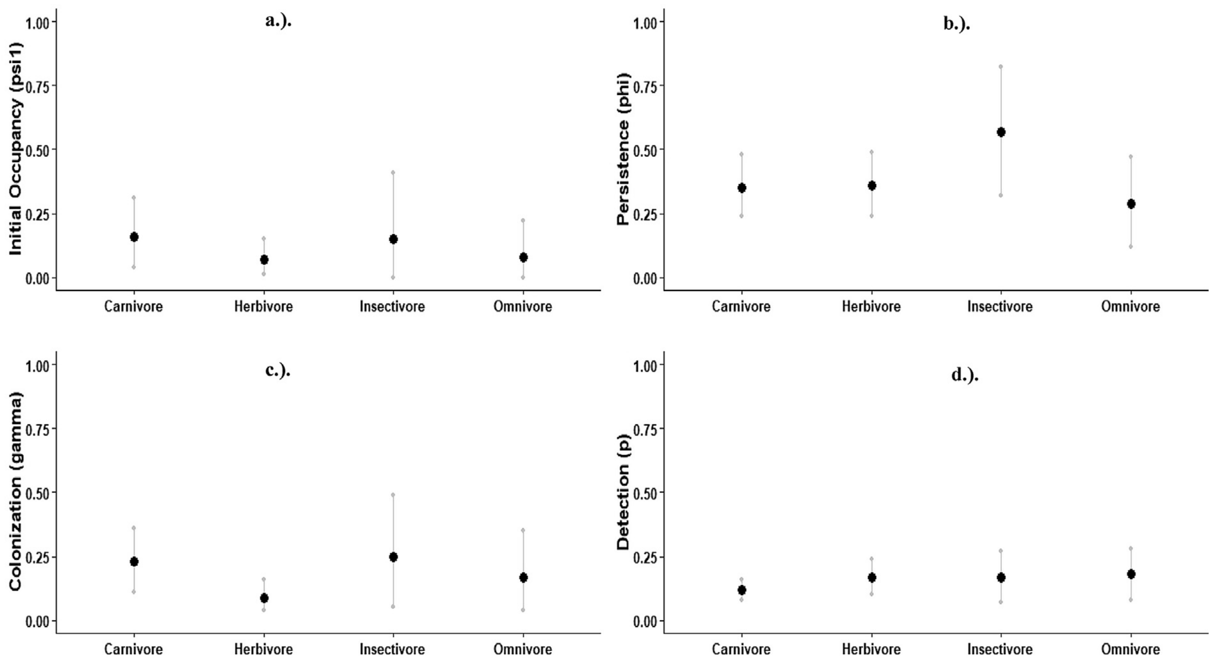

Fig. 3. Bar-plots of estimated mean detectability, occupancy, persistence and colonization of four dietary guilds in Nam Et - Phou Louey National Protected Area, Laos, during 2013–2017.

Table 3
Predicted species number that could be detected each year by camera trapping from 2013 to 2017 in Nam Et - Phou Louey National Protected Area, Laos.

	Mean	SD	CI
Y1	39.20	1.20	37–41
Y2	43.00	0.20	43–43
Y3	42.80	0.50	42–43

Y: year; SD: standard deviation, CI: Bayesian credible interval.

4. Discussion

Prompted by reports that levels of snaring were unsustainable, and mindful of the national, indeed regional importance of NEPL as an important source population for tiger (Johnson et al., 2016) and dhole (Kamler et al., 2012), we conducted the largest camera trapping survey ever attempted in Laos. While we have no counter-factual to judge how much worse things might have been, our results make sadly apparent that the last decade of management interventions has fallen short of the goal of conserving of the top carnivores: conspicuously, tiger and leopard have been extirpated, and only the dhole persists as the last remaining apex carnivore in the landscape. The last photograph of a leopard from NEPL was at the end of 2004 (Rostro-García et al., 2016), shortly before the initiation of management interventions at the beginning of 2005 (Johnson et al., 2016); thus our extensive camera-trap surveys confirm that the leopard is extirpated from NEPL and that the new management interventions were not able to save the last leopards in the landscape. It appears we recorded the very last tigers, two individuals that had previously been photographed in 2012 (Johnson et al., 2016) – it is a chilling realisation that our records in 2013 were the last. That they abruptly disappeared from the survey areas within NEPL after 2013 suggests they died, probably because of the increase in snaring (Johnson et al., 2016), rather than they dispersed from the site or somehow remained undetected in subsequent years. Both tiger and leopard are readily photographed in camera traps when they are present in an area, thus their conspicuous absence in our extensive camera-trap surveys is strong evidence that both no longer persist in NEPL. The last records of leopard and tiger in Laos were from NEPL, and the threatening factors in NEPL are more or less ubiquitous in Laos; thus, it is unlikely that any large, undetected population of either persists anywhere in the country. That said, the extirpations of leopard and tiger in NEPL were very late in the Lao context, and various other hunting-sensitive species (e.g., clouded leopard, sun bear, sambar) are still doing relatively well in NEPL compared with other protected areas in Laos.

The extirpation of tiger, and possibly leopard, in NEPL was likely to have been related to the exponential increase in snaring in NEPL, which occurred despite increases in enforcement activities (Johnson et al., 2016). Indiscriminate snaring has been increasing throughout SE Asia during recent years, which is causing a major crisis for biodiversity in the region (Gray et al., 2017b). For example, this was likely to have been the main reason for the recent range collapse of leopard throughout Southeast Asia (Rostro-García et al., 2016). The increase in snaring in NEPL was likely to affect large felids such as tiger more than other species, as also found in Sumatra (Risdianto et al., 2016), because large felids are solitary and have naturally low densities. Additionally, large felids have wide ranging movements and thus probably had the largest home ranges of any mammal in the landscape, making them the most susceptible to the increasing numbers of snares, even if snares were primarily set in the buffer zones.

In contrast to large felids, the dhole, along with smaller carnivores and ungulates, have persisted in NEPL during the last decade. Additionally, we detected two species of primates, northern pig-tailed macaque *Macaca leonina* and Rhesus macaque *Macaca mulatta*, that were not detected in the previous camera-trap surveys. However, these two primate species had low probability of initial occupancy, persistence and colonization, suggesting their absence from previous surveys might have been due to the lower camera-trapping effort. With the absence of leopard and tiger within NEPL, dhole may have prospered, possibly because of mesopredator release (Karanth and Sunquist, 1995, 2000). For example, in our survey dhole were detected in all survey blocks, whereas in 2003 dhole was absent only from the survey block where leopard was detected (Johnson et al., 2006). Additionally, the records of dhole increased two-fold from the first to the last years of our survey in block 1 (NV) which is also the block where 90% of the tiger records occurred in 2013.

Our findings show that clouded leopard is the most widespread species of carnivore in the NEPL, mirroring the earlier results of Johnson et al. (2006). In contrast, Asian golden cat was the least widespread meso-felid having a mean rate of occupancy (0.37 ± 0.13), which also was similar to that previously reported 0.42 ± 0.14 (Johnson et al., 2009). Although it is unclear why clouded leopard has remained more widespread than Asian gold cat in NEPL, our findings suggest that both meso-felids were unaffected by changes in the presence and occupancy of the large carnivores.

Our results showed that marbled cat and leopard cat have increased since the surveys in 2003 (Johnson et al., 2006). These small felids eat mostly rodents (Rajaratnam et al., 2007; Ross et al., 2016), of which we detected 10 species. However, differences in camera-trap models and sensitivity settings, along with differences in classification protocols for small rodents, preclude a comparison of small rodent diversity and abundance between our study and that of Johnson et al. (2006). Thus, it is unclear why both small felids seemingly increased in NEPL during the past decade, although they must have benefited from the last 10 years of management.

Similar to Johnson et al. (2006), we detected 11 other small carnivores in the families Mustelidae, Viverridae, Herpestidae and Prionodontidae, although some of the species differed. For example, we detected the ferret badger(s) *Melogale* spp. and binturong *Arctictis binturong*, which were not detected in the previous survey (Johnson et al., 2006). In contrast, Johnson et al. (2006) detected the striped-backed weasel *Mustela strigidorsa* and oriental small-clawed otter *Aonyx cinereus*, which were not detected in our surveys. This guild of Asian carnivores is poorly known (Macdonald et al., 2017a), and we are unsure if changes in species detections between studies represent actual differences in presence/absence, or simply chance photographs of small species with low densities. Nonetheless, our DCM results suggested an increase in occupancy rate for most species in this group, except for Owston's civet *Chrotogale owstoni*, small Indian civet *Viverricula indica* and spotted linsang *Prionodon pardicolor*.

Sun bear was more widespread in the NEPL than Asian black bear based on our camera-trap survey. In contrast, Scotson (2010) had concluded that sun bear occurred in NEPL at a lower density than black bear based on field sign surveys. This could be true at the time when the previous study was conducted, but it could also be that the signs were recorded opportunistically and thus did not reflect actual differences in abundance (Scotson, 2010). One possibility is that Asian black bear had declined since the survey by Scotson (2010), because this bear species is more prone to capture in snares compared with sun bear; Asian black bear is more tolerant of human disturbed habitat and is found to wander closer to human settlements (Ngoprasert et al., 2011; Garshelis and Steinmetz, 2016). In contrast, sun bear is forest dependent species and prefer areas further from humans (Scotson et al., 2017). Based on our DCM results, sun bear was more persistent, with a colonization rate twice that of black bear. However, both bear species are threatened by overhunting for commercial trade for their paws and gall bladders for traditional Asian medicine (Livingstone and Shepherd, 2014).

We documented the occurrence of potential prey for large and medium-sized carnivores: northern red muntjac, stump-tailed macaque, Eurasian wild pig, silver pheasant, Indochinese serow and small dark muntjac(s). Reversing the findings of Johnson et al. (2006), we found red muntjac to be much more widespread than stump-tailed macaque. Among large species of potential prey, wild pig was most widespread, followed by Indochinese serow. Wild pig is overall the most preferred prey of tiger (Hayward et al., 2012), and wild pig remained widely distributed in NEPL, which further supports our conclusion that tiger became extirpated because of the increase in snaring (Johnson et al., 2016), rather than for other reasons such as prey declines.

5. Conservation implications

We provide a flexible analytical framework for the incorporation of sparse, inconsistent yet valuable data sets on multiple species to assess their status via occupancy as a state process, offering scope to infer population dynamics over time. This study provides the most recent assessment of animal diversity and status in the NEPL, Laos. Regrettably, the most striking finding is that tiger and leopard are likely to have been extirpated from the NEPL, and probably from Laos. This has important implications for tiger conservation planning in Southeast Asia, because NEPL was identified as the last remaining source site for tiger in all of Laos, Cambodia, and Vietnam (Walston et al., 2010), thus in lieu of reintroductions (Gray et al., 2017a), conservation efforts in the region should now focus on remaining viable populations in other countries, such as Thailand, Malaysia, Myanmar, and Indonesia (Sumatra). Of the remaining species in NEPL, clouded leopard and dhole are the only remaining apex carnivores, thus their conservation in the landscape should become a priority. Maintaining these species in the landscape will help prevent trophic cascades caused by the loss of top carnivores (Terborgh and Estes, 2013). The clouded leopard in particular is charismatic and has the potential to act as an ambassador species for conservation (*sensu* Macdonald et al., 2017b). Finally, other species that are extremely rare in the region, but that we recorded in NEPL (e.g., Owston's civet, small dark muntjac species), should become conservation priorities because their populations in NEPL are an important part of their global populations.

Authors' contributions

A.R., conceived the ideas, designed methodology, collected and analysed the data, interpreted analysis results and led the writing of the manuscript. M.K., helped with the design of methodology, interpretation of the analysis results and checking of the manuscript. J.K., D.W.M, supervised the research, checked the manuscript contents and references. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

We thank the Wildlife Conservation Society and the Nam Et - Phou Louey National Protected Area for their extensive in-kind support. We further thank Mr. Phonesouk Chanthalavong for his assistance and Dr. Lucy Talents for her guidance. We deeply grateful for the Exploration Grant from the National Geographic and a grant to DWM from the Robertson Foundation.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00766.

Appendix B

Table A.1
List of species detected and number of observed occupied stations for each species across three survey years during 2013–2017 in Nam Et - Phou Louey National Protected Area.

Species (Scientific name)	Species (Common name)	Y1	Y2	Y3
Ursus thibetanus	Asian black bear	4	2	5
Atherurus macrourus	Asian brush-tailed porcupine	18	19	20
Catopuma temminckii	Asian golden cat	49	28	27
Macaca assamensis	Assamese macaque	15	7	7
Arctictis binturong	Binturong	4	9	3
Ratufa bicolor	Black giant squirrel	1	3	3
Paradoxurus hermaphroditus	Common palm civet	2	48	37
Herpestes urva	Crab-eating mongoose	26	42	33
Cuon alpinus	Dhole	41	63	60
Hystrix brachyura	East Asian porcupine	61	7	35
Sus scrofa	Eurasian wild pig	75	37	32
Melogale spp.	Ferret badger(s)	4	2	6
Bos gaurus	Gaur	1	1	0
Arctonyx collaris	Greater hog badger	62	39	74
Polyplectron bicalcaratum	Grey peacock pheasant	13	22	30
Capricornis milneedwardsii	Indochinese serow	55	42	37
Viverra zibetha	Large Indian civet	48	59	51
Prionailurus bengalensis	Leopard cat	34	43	30
Neofelis nebulosa	Mainland clouded leopard	41	37	24
Pardofelis marmorata	Marbled cat	29	27	24
Paguma larvata	Masked palm civet	41	45	44
Macaca leonina	Northern pig-tailed macaque	6	3	6
Muntiacus vaginalis	Northern red muntjac	168	134	106
Chrotogale owstoni	Owston's civet	8	13	25
Callosciurus erythraeus and/or *C. inornatus*	Pallas's and/or Inornate Squirrel	1	4	2
	Rat morphotype 1	0	17	22
	Rat morphotype 2	5	0	18
	Rat morphotype 3	0	5	0
Gallus gallus	Red junglefowl	11	5	31
Macaca mulatta	Rhesus macaque	12	5	0
Cervus unicolor	Sambar	24	14	9
Lophura nycthemera	Silver pheasant	50	37	47
M. rooseveltorum complex	Small dark muntjac(s)	32	17	33
Viverricula indica	Small Indian civet	2	4	9
Prionodon pardicolor	Spotted linsang	6	7	15
	Squirrel morphotype 1	0	0	3
	Squirrel morphotype 2	0	14	15
Tamiops complex	Striped squirrel(s)	0	2	0
Macaca arctoides	Stump-tailed macaque	105	49	87
Helarctos malayanus	Sun bear	28	47	29
Panthera tigris	Tiger	14	0	0
Arborophila rufogularis	Unknown partridge	0	7	20
Martes flavigula	Yellow-throated marten	77	69	65

Table A.2
Estimated mean initial occupancy probabilities (psi1) of species detected in Nam Et - Phou Louey National Protected Area during 2013–2017

Species (Scientific name)	Species (Common name)	psi1	sd	CrI
Ursus thibetanus	Asian black bear	0.090	0.105	0–0.289
Atherurus macrourus	Asian brush-tailed porcupine	0.074	0.032	0.019–0.129
Catopuma temminckii	Asian golden cat	0.371	0.128	0.122–0.631
Macaca assamensis	Assamese macaque	0.096	0.071	0.002–0.224
Arctictis binturong	Binturong	0.101	0.095	0.004–0.29
Ratufa bicolor	Black giant squirrel	0.013	0.017	0–0.04
Paradoxurus hermaphroditus	Common palm civet	0.015	0.023	0–0.043
Herpestes urva	Crab-eating mongoose	0.121	0.100	0.002–0.313

(*continued on next page*)

Table A.2 (*continued*)

Species (Scientific name)	Species (Common name)	psi1	sd	CrI
Cuon alpinus	Dhole	0.156	0.101	0.006–0.346
Hystrix brachyura	East Asian porcupine	0.286	0.067	0.15–0.417
Sus scrofa	Eurasian wild pig	0.428	0.120	0.178–0.665
Melogale spp.	Ferret badger(s)	0.041	0.037	0.001–0.107
Bos gaurus	Gaur	0.027	0.051	0–0.095
Arctonyx collaris	Greater hog badger	0.297	0.130	0.061–0.559
Polyplectron bicalcaratum	Grey peacock pheasant	0.072	0.065	0.001–0.186
Capricornis milneedwardsii	Indochinese serow	0.317	0.147	0.035–0.596
Viverra zibetha	Large Indian civet	0.237	0.076	0.082–0.382
Prionailurus bengalensis	Leopard cat	0.204	0.088	0.04–0.374
Neofelis nebulosa	Mainland clouded leopard	0.512	0.176	0.181–0.875
Pardofelis marmorata	Marbled cat	0.228	0.128	0.023–0.481
Paguma larvata	Masked palm civet	0.238	0.135	0.016–0.496
Macaca leonina	Northern pig-tailed macaque	0.058	0.071	0–0.185
Muntiacus vaginalis	Northern red muntjac	0.684	0.071	0.553–0.817
Chrotogale owstoni	Owston's civet	0.025	0.030	0–0.07
Callosciurus erythraeus and/or *C. inornatus*	Pallas's and/or Inornate Squirrel	0.025	0.036	0–0.083
	Rat morphotype 1	0.005	0.013	0–0.017
	Rat morphotype 2	0.027	0.030	0–0.075
	Rat morphotype 3	0.005	0.011	0–0.015
Gallus gallus	Red junglefowl	0.097	0.081	0.002–0.247
Macaca mulatta	Rhesus macaque	0.079	0.040	0.017–0.15
Cervus unicolor	Sambar	0.108	0.039	0.038–0.183
Lophura nycthemera	Silver pheasant	0.329	0.116	0.103–0.568
M. rooseveltorum complex	Small dark muntjac(s)	0.386	0.144	0.128–0.69
Viverricula indica	Small Indian civet	0.019	0.020	0–0.052
Prionodon pardicolor	Spotted linsang	0.059	0.041	0.004–0.132
	Squirrel morphotype 1	0.007	0.015	0–0.028
	Squirrel morphotype 2	0.005	0.009	0–0.017
Tamiops complex	Striped squirrel(s)	0.006	0.012	0–0.021
Macaca arctoides	Stump-tailed macaque	0.558	0.099	0.349–0.76
Helarctos malayanus	Sun bear	0.178	0.075	0.043–0.321
Panthera tigris	Tiger	0.202	0.212	0.001–0.711
Arborophila rufogularis	Unknown partridge	0.005	0.011	0–0.018
Martes flavigula	Yellow-throated marten	0.332	0.075	0.173–0.481

Table A.3
Estimated mean persistence probabilities (phi) of species detected in Nam Et - Phou Louey National Protected Area during 2013–2017

Species (Scientific name)	Species (Common name)	phi	sd	CrI
Ursus thibetanus	Asian black bear	0.315	0.174	0.032–0.659
Atherurus macrourus	Asian brush-tailed porcupine	0.317	0.085	0.161–0.486
Catopuma temminckii	Asian golden cat	0.430	0.106	0.23–0.636
Macaca assamensis	Assamese macaque	0.349	0.121	0.121–0.581
Arctictis binturong	Binturong	0.308	0.167	0.042–0.643
Ratufa bicolor	Black giant squirrel	0.382	0.159	0.098–0.696
Paradoxurus hermaphroditus	Common palm civet	0.275	0.078	0.128–0.427
Herpestes urva	Crab-eating mongoose	0.330	0.087	0.171–0.505
Cuon alpinus	Dhole	0.535	0.065	0.408–0.661
Hystrix brachyura	East Asian porcupine	0.152	0.053	0.059–0.258
Sus scrofa	Eurasian wild pig	0.309	0.069	0.177–0.444
Melogale spp.	Ferret badger(s)	0.294	0.145	0.049–0.582
Bos gaurus	Gaur	0.331	0.161	0.052–0.645
Arctonyx collaris	Greater hog badger	0.513	0.072	0.37–0.651
Polyplectron bicalcaratum	Grey peacock pheasant	0.509	0.134	0.251–0.764
Capricornis milneedwardsii	Indochinese serow	0.452	0.071	0.311–0.589
Viverra zibetha	Large Indian civet	0.379	0.063	0.261–0.506
Prionailurus bengalensis	Leopard cat	0.372	0.079	0.22–0.529
Neofelis nebulosa	Mainland clouded leopard	0.538	0.130	0.29–0.789
Pardofelis marmorata	Marbled cat	0.304	0.100	0.126–0.507
Paguma larvata	Masked palm civet	0.388	0.084	0.232–0.558
Macaca leonina	Northern pig-tailed macaque	0.330	0.162	0.044–0.642
Muntiacus vaginalis	Northern red muntjac	0.708	0.036	0.637–0.778
Chrotogale owstoni	Owston's civet	0.132	0.074	0.013–0.275
Callosciurus erythraeus and/or *C. inornatus*	Pallas's and/or Inornate Squirrel	0.394	0.166	0.107–0.73

Table A.3 (*continued*)

Species (Scientific name)	Species (Common name)	phi	sd	CrI
	Rat morphotype 1	0.423	0.128	0.194–0.688
	Rat morphotype 2	0.286	0.133	0.056–0.554
	Rat morphotype 3	0.208	0.120	0.015–0.44
Gallus gallus	Red junglefowl	0.675	0.164	0.355–0.962
Macaca mulatta	Rhesus macaque	0.334	0.123	0.1–0.57
Cervus unicolor	Sambar	0.311	0.082	0.151–0.469
Lophura nycthemera	Silver pheasant	0.540	0.109	0.333–0.756
M. rooseveltorum complex	Small dark muntjac(s)	0.306	0.135	0.077–0.575
Viverricula indica	Small Indian civet	0.391	0.162	0.093–0.699
Prionodon pardicolor	Spotted linsang	0.354	0.148	0.092–0.652
	Squirrel morphotype 1	0.379	0.178	0.062–0.721
	Squirrel morphotype 2	0.266	0.122	0.052–0.504
Tamiops complex	Striped squirrel(s)	0.313	0.158	0.034–0.615
Macaca arctoides	Stump-tailed macaque	0.431	0.054	0.329–0.539
Helarctos malayanus	Sun bear	0.439	0.090	0.267–0.617
Panthera tigris	Tiger	0.155	0.081	0.023–0.315
Arborophila rufogularis	Unknown partridge	0.564	0.182	0.215–0.897
Martes flavigula	Yellow-throated marten	0.529	0.056	0.419–0.641

Table A.4
Estimated mean colonization probabilities (gamma) of species detected in Nam Et - Phou Louey National Protected Area during 2013–2017

Species (Scientific name)	Species (Common name)	gamma	sd	CrI
Ursus thibetanus	Asian black bear	0.136	0.128	0.013–0.405
Atherurus macrourus	Asian brush-tailed porcupine	0.090	0.016	0.059–0.122
Catopuma temminckii	Asian golden cat	0.242	0.065	0.127–0.374
Macaca assamensis	Assamese macaque	0.049	0.019	0.016–0.085
Arctictis binturong	Binturong	0.207	0.188	0.01–0.664
Ratufa bicolor	Black giant squirrel	0.029	0.017	0.005–0.062
Paradoxurus hermaphroditus	Common palm civet	0.305	0.039	0.228–0.38
Herpestes urva	Crab-eating mongoose	0.349	0.063	0.232–0.472
Cuon alpinus	Dhole	0.378	0.045	0.291–0.466
Hystrix brachyura	East Asian porcupine	0.142	0.024	0.095–0.19
Sus scrofa	Eurasian wild pig	0.290	0.055	0.187–0.4
Melogale spp.	Ferret badger(s)	0.055	0.030	0.013–0.11
Bos gaurus	Gaur	0.024	0.040	0–0.079
Arctonyx collaris	Greater hog badger	0.343	0.041	0.263–0.423
Polyplectron bicalcaratum	Grey peacock pheasant	0.174	0.030	0.119–0.234
Capricornis milneedwardsii	Indochinese serow	0.282	0.050	0.186–0.382
Viverra zibetha	Large Indian civet	0.373	0.045	0.286–0.463
Prionailurus bengalensis	Leopard cat	0.304	0.053	0.202–0.408
Neofelis nebulosa	Mainland clouded leopard	0.507	0.165	0.23–0.871
Pardofelis marmorata	Marbled cat	0.342	0.107	0.168–0.554
Paguma larvata	Masked palm civet	0.451	0.084	0.307–0.627
Macaca leonina	Northern pig-tailed macaque	0.078	0.061	0.011–0.177
Muntiacus vaginalis	Northern red muntjac	0.605	0.066	0.477–0.735
Chrotogale owstoni	Owston's civet	0.123	0.020	0.085–0.164
Callosciurus erythraeus and/or *C. inornatus*	Pallas's and/or Inornate Squirrel	0.063	0.061	0.003–0.173
	Rat morphotype 1	0.134	0.024	0.088–0.182
	Rat morphotype 2	0.086	0.024	0.043–0.132
	Rat morphotype 3	0.022	0.010	0.005–0.041
Gallus gallus	Red junglefowl	0.189	0.045	0.11–0.277
Macaca mulatta	Rhesus macaque	0.012	0.008	0–0.027
Cervus unicolor	Sambar	0.048	0.014	0.023–0.075
Lophura nycthemera	Silver pheasant	0.355	0.069	0.231–0.495
M. rooseveltorum complex	Small dark muntjac(s)	0.451	0.154	0.209–0.786
Viverricula indica	Small Indian civet	0.059	0.020	0.023–0.097
Prionodon pardicolor	Spotted linsang	0.133	0.047	0.057–0.224
	Squirrel morphotype 1	0.033	0.031	0.002–0.088
	Squirrel morphotype 2	0.127	0.032	0.069–0.187
Tamiops complex	Striped squirrel(s)	0.016	0.012	0.001–0.039
Macaca arctoides	Stump-tailed macaque	0.588	0.057	0.478–0.704

(*continued on next page*)

Table A.4 (*continued*)

Species (Scientific name)	Species (Common name)	gamma	sd	CrI
Helarctos malayanus	Sun bear	0.314	0.060	0.209–0.436
Panthera tigris	Tiger	0.023	0.029	0–0.072
Arborophila rufogularis	Unknown partridge	0.096	0.022	0.057–0.141
Martes flavigula	Yellow-throated marten	0.351	0.041	0.272–0.43

Table A.5
Estimated mean detection probabilities (p) of species detected in Nam Et - Phou Louey National Protected Area during 2013–2017

Species (Scientific name)	Species (Common name)	p	sd	CrI
Ursus thibetanus	Asian black bear	0.102	0.065	0.011–0.231
Atherurus macrourus	Asian brush-tailed porcupine	0.288	0.092	0.109–0.444
Catopuma temminckii	Asian golden cat	0.116	0.026	0.067–0.167
Macaca assamensis	Assamese macaque	0.146	0.043	0.063–0.23
Arctictis binturong	Binturong	0.064	0.037	0.011–0.136
Ratufa bicolor	Black giant squirrel	0.144	0.065	0.032–0.269
Paradoxurus hermaphroditus	Common palm civet	0.217	0.043	0.122–0.296
Herpestes urva	Crab-eating mongoose	0.146	0.042	0.067–0.226
Cuon alpinus	Dhole	0.188	0.062	0.072–0.309
Hystrix brachyura	East Asian porcupine	0.229	0.058	0.114–0.343
Sus scrofa	Eurasian wild pig	0.162	0.034	0.094–0.224
Melogale spp.	Ferret badger(s)	0.111	0.048	0.029–0.206
Bos gaurus	Gaur	0.117	0.07	0.01–0.252
Arctonyx collaris	Greater hog badger	0.193	0.053	0.088–0.295
Polyplectron bicalcaratum	Grey peacock pheasant	0.181	0.047	0.086–0.268
Capricornis milneedwardsii	Indochinese serow	0.164	0.054	0.069–0.275
Viverra zibetha	Large Indian civet	0.183	0.066	0.061–0.307
Prionailurus bengalensis	Leopard cat	0.152	0.035	0.08–0.221
Neofelis nebulosa	Mainland clouded leopard	0.074	0.025	0.033–0.119
Pardofelis marmorata	Marbled cat	0.106	0.028	0.056–0.16
Paguma larvata	Masked palm civet	0.138	0.035	0.071–0.21
Macaca leonina	Northern pig-tailed macaque	0.091	0.045	0.016–0.179
Muntiacus vaginalis	Northern red muntjac	0.306	0.056	0.179–0.403
Chrotogale owstoni	Owston's civet	0.274	0.067	0.122–0.393
Callosciurus erythraeus and/or *C. inornatus*	Pallas's and/or Inornate Squirrel	0.109	0.062	0.014–0.23
	Rat morphotype 1	0.196	0.087	0.051–0.371
	Rat morphotype 2	0.155	0.068	0.037–0.291
	Rat morphotype 3	0.223	0.1	0.047–0.418
Gallus gallus	Red junglefowl	0.117	0.05	0.038–0.214
Macaca mulatta	Rhesus macaque	0.168	0.054	0.066–0.273
Cervus unicolor	Sambar	0.242	0.073	0.102–0.378
Lophura nycthemera	Silver pheasant	0.14	0.027	0.088–0.193
M. rooseveltorum complex	Small dark muntjac(s)	0.085	0.031	0.032–0.145
Viverricula indica	Small Indian civet	0.129	0.059	0.031–0.245
Prionodon pardicolor	Spotted linsang	0.103	0.037	0.039–0.175
	Squirrel morphotype 1	0.133	0.073	0.016–0.274
	Squirrel morphotype 2	0.174	0.063	0.06–0.297
Tamiops complex	Striped squirrel(s)	0.176	0.093	0.026–0.36
Macaca arctoides	Stump-tailed macaque	0.19	0.067	0.068–0.324
Helarctos malayanus	Sun bear	0.148	0.04	0.075–0.227
Panthera tigris	Tiger	0.083	0.045	0.009–0.169
Arborophila rufogularis	Unknown partridge	0.196	0.061	0.083–0.317
Martes flavigula	Yellow-throated marten	0.244	0.067	0.099–0.361

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