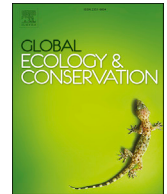




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Original Research Article

# Density and movements of mainland clouded leopards (*Neofelis nebulosa*) under conditions of high and low poaching pressure

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## ABSTRACT

Despite its high risk of extinction in the wild, little is known about the ecology and population status of the mainland clouded leopard (*Neofelis nebulosa*). We used camera-traps and spatial capture-recapture analysis to estimate mainland clouded leopard density within southern Thailand's Khlong Saeng – Khao Sok Forest Complex, comparing densities in two zones of the forest with different levels of human access and poaching pressure (core and edge). Over 5242 trap-days, we detected at least 27 mainland clouded leopards, including 12 females and 15 males. Model averaged density in the less accessible core zone ( $5.06 \pm SE 1.64/100 \text{ km}^2$ ) was 62% higher compared to the more accessible and more heavily hunted edge zone ( $3.13 \pm SE 1.05/100 \text{ km}^2$ ). This density difference corresponded to a 56% higher occupancy probability of muntjacs (*Muntiacus* spp.) in the core zone, a potentially important prey species for clouded leopards. Model averaged movements (sigma) of male clouded leopards were 38% larger (3448 m; SE 551 m) than female movements (2502 m; SE 478 m). Mainland clouded leopard density at our study site was among the highest recorded in South and Southeast Asia (range: 0.40 to 5.14/100 km<sup>2</sup>). We hypothesize this high density might be related to the extirpation of larger sympatric carnivores. Our study provides important baseline information for monitoring the conservation status of mainland clouded leopards in Thailand and Southeast Asia and offers insights into the species' behavioral ecology and capacity to adapt to human disturbance. © 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

## 1. Introduction

Mainland clouded leopards (*Neofelis nebulosa*, “clouded leopard”) are one of the least studied felids in Southeast Asia. Classified as Vulnerable under the IUCN Red List, the clouded leopard faces a high risk of extinction in the wild, due largely to habitat loss (Grassman et al., 2016). Clouded leopards are also commonly traded in the black market, suggesting the species

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may face substantial hunting pressure for its pelt and other parts (Martin, 1997; Sheperd and Nijman, 2008; Oswell, 2010; Jenks et al., 2012). Despite these threats, little is known about the ecology and population status of clouded leopards, nor how the species responds to human disturbance and prey depletion—two potential threats known to have profound effects on other carnivores (e.g., Baker and Leberg, 2018; Carter et al., 2019). Indeed, prey depletion caused by poaching is a well-publicized and pervasive problem for large carnivores in Southeast Asia (Wolf and Ripple, 2016), yet its effects on clouded leopards are unknown.

In this paper, we present density estimates for clouded leopards in southern Thailand's Khlong Saeng – Khao Sok Forest Complex, using camera-trap data collected from 2016 to 2017. Based on the knowledge of park rangers and patrol data, we divided the study area into core and edge zones, reflecting different levels of human access and poaching pressure. Over the past 9 years, there have been 33 criminal cases involving wildlife poaching within the edge zone, versus 12 cases in the core (Appendix 1). An additional unknown number of poaching incidents probably go undetected, but patrol effort is higher in the core zone (Khlong Saeng Wildlife Sanctuary, unpublished report, 2019), so these data indicate a substantial difference in poaching levels. Rangers report that poachers primarily use guns to hunt, and snares are rarely encountered during patrols. Species targeted by hunters include three potential prey species of clouded leopards: mouse deer (*Tragulid* spp.), muntjac (*Muntiacus* spp.), and wild boar (*Sus scrofa*); but not clouded leopards themselves (K. Sribuarod, pers.comm.; W. Saengthong, Khao Sok National Park, pers. comm.).

We made three predictions. First, the core should support higher prey availability compared to the edge, due to lower levels of human access and poaching, especially for wild boar, muntjacs, and mouse deer, with no substantial differences in core and edge occupancy probabilities expected for other potential prey species. Second, we predicted clouded leopard density would be higher in the zone with higher prey availability, as prey availability has been shown to correlate with the density of other wild felids (e.g., Karanth et al., 2004; Hetherington and Gorman, 2007). Third, clouded leopards should exhibit more widespread movements in the zone where prey were scarcer, because carnivore home range sizes and ranging patterns tend to increase as resource abundance declines (Fuller and Sievert, 2001). We used sigma ( $\sigma$ ), the scale of movement parameter estimated in spatially explicit capture-recapture (SECR) models, as a measure of clouded leopard movements. Finally, we collated all available studies on clouded leopard density to better understand differences in the site-specific ecology and population status of clouded leopards.

## 2. Material and methods

### 2.1. Study area

The Khlong Saeng – Khao Sok Forest Complex (“Khlong Saeng”) in peninsular Thailand (9° 10' N 98° 35' E) covers 4693 km<sup>2</sup> of protected forest. The complex consists of four national parks and three wildlife sanctuaries, with Khlong Saeng Wildlife Sanctuary (1156 km<sup>2</sup>) and Khao Sok National Park (739 km<sup>2</sup>) the two largest protected areas. The dominant forest type is semi-evergreen forest. Elevation ranges from 100 to 1395 m above sea level. A rainy season occurs from April to November and a dry season from December to March. Annual rainfall averages 1700 mm but can exceed 3500 mm in some years (Electricity Generating Authority of Thailand, 1980).

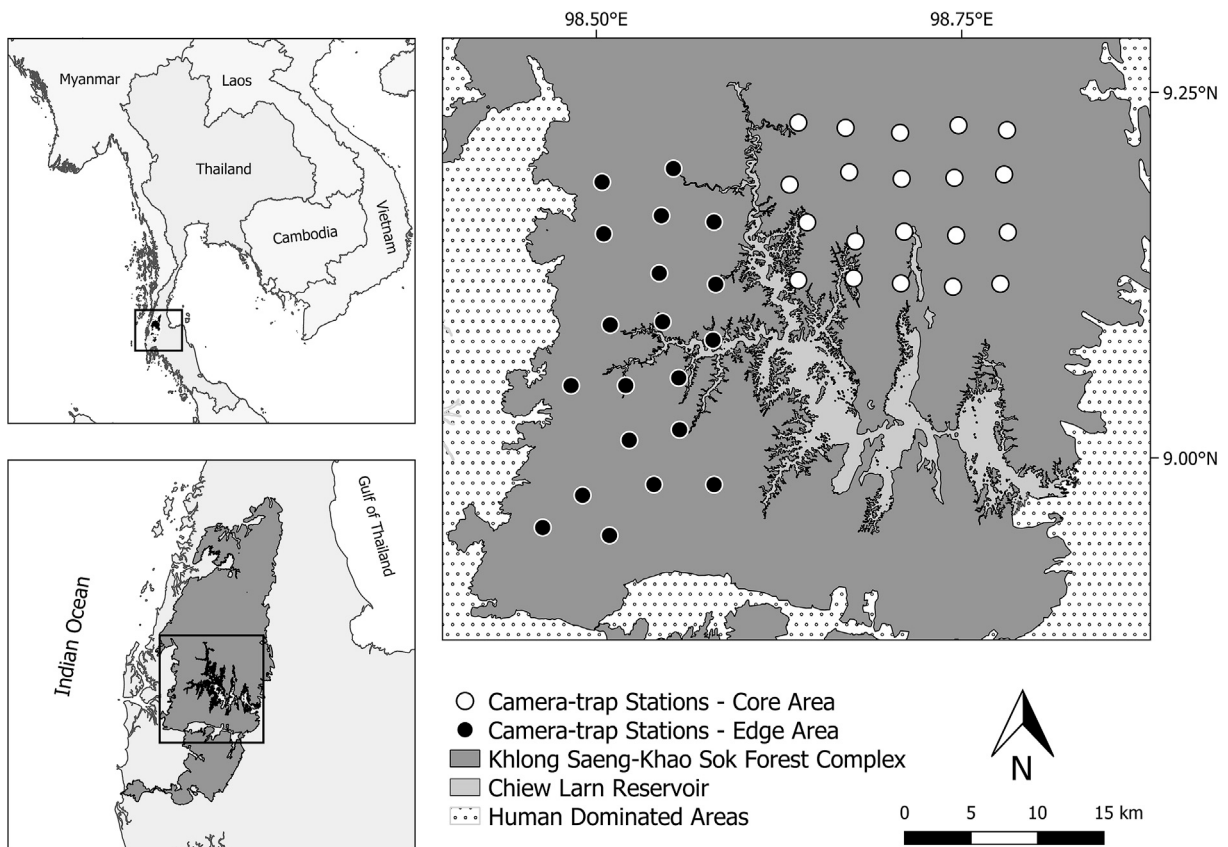
Despite being the largest forest complex in southern Thailand, Khlong Saeng's carnivore community has undergone drastic changes. Tigers (*Panthera tigris*) and dholes (*Cuon alpinus*) have not been observed for 19 years (Kanchanasaka, 2001). A single leopard (*P. pardus*) was documented in 2014 (Rostro-García et al., 2016), however, our work, as well as more recent surveys specifically targeting leopards, have failed to detect that species (R. Sukmasuang, pers. comm, 2019). As such, clouded leopards appear to be Khlong Saeng's largest remaining obligate carnivore.

### 2.2. Camera-trapping

Twenty camera-stations, spaced approximately 3.5 km apart, were set up in both core and edge zones (40 stations total; Fig. 1). Camera-traps (Scout Guard SG565) were deployed in the core zone from February 2016 to June 2016 and in the edge zone from December 2016 to May 2017; both periods were during the dry season. Camera-trap surveys in Khlong Saeng were designed to capture bears (*Ursus thibetanus*, *Helarctos malayanus*) and other large mammals. Three camera-traps were mounted on trees 3–4 m apart and facing each other in a triangular arrangement, with a non-reward bait (5 kg of beef, “bait”) suspended 2 m above the ground in the center (Ngoprasert et al., 2012a). Camera-stations were primarily set on ridges, which are used by many wildlife species for movement. Camera-traps were set to take continuous still pictures, with no delay between triggers. Cameras were left active 24 h a day. We changed the bait, batteries, and memory cards once per month. Photographs from camera-traps were considered notionally independent if the time between photographs was  $\geq 30$  min (O'Brien et al., 2003).

### 2.3. Prey availability

We reviewed the literature for available data concerning clouded leopard diet. Known prey species include small and medium sized ungulates (northern red muntjac *M. vaginalis*, hog deer *Axis porcinus*, and mouse deer *Tragulid* spp.; Grassman et al., 2005), primates (northern pig-tailed macaque *Macaca leonina*, Davies, 1990; leaf monkeys *Trachypithecus* spp., slow loris



**Fig. 1.** Location and map of southern Thailand's Khlong Saeng – Khao Sok Forest Complex, including locations of core and edge camera-trap stations used during our study.

*Nycticebus bengalensis*; Grassman et al., 2005), pangolins (*Manis javanica*, Grassman et al., 2005), small carnivores (binturong *Arctictis binturong*, Lam et al., 2014) and rodents (brush-tailed porcupine *Atherurus macrourus*, Berdmore's ground squirrel *Menetes berdmorei*, murids *Muridae*; Grassman et al., 2005). Our camera-traps detected several of these known prey species, as well as other similar species that are likely to be prey (e.g., southern pig-tailed macaques *M. nemestrina*). Detections of most confirmed and potential prey species were sparse, except for muntjac and wild boar, therefore we grouped species into six prey groups based on phylogenetic and ecological similarities: macaques (southern pig-tailed macaque, stump-tailed macaque *M. arctoides*), small carnivores (*A. binturong*, banded civet *Hemigalus derbyanus*, yellow-throated marten *Martes flavigula*, masked palm civet *Paguma lavarta*, common palm civet *Paradoxurus hermaphroditus*), porcupines (Malayan porcupine *Hystrix brachyura*, *A. macrourus*), mouse deer (lesser mouse deer *T. kanchil*, greater mouse deer *T. napu*), muntjacs, and wild boar. We did not expect clouded leopards to prey on species which can exceed 100 kg (i.e., *Bos gaurus*, *Capricornis sumatraensis*, *Elephas maximus*, *Rusa unicolor*, *Tapirus indicus*) or on smaller sympatric felids (i.e., *Catopuma temminckii*, *Pardofelis marmorata*, *Prionailurus bengalensis*); these species were thus not included as potential prey.

We used an occupancy-based approach to quantify relative prey availability, due to the potential for variation in the detectability of different prey species. We estimated site-occupancy probabilities for the aforementioned prey groups by fitting single-season multispecies occupancy models for the four groups with more than one species, and single-season single species occupancy models for muntjac and wild boar (Dorazio et al., 2006; MacKenzie et al., 2006). We used daily occasions for detection histories, with occasions beginning 0000 h and ending at 2359 h. Occupancy models were implemented within a Bayesian framework using program JAGS (version 3.4.0; Plummer, 2003), interfaced through program R (version 3.6.0; R Development Core Team, 2019) using package 'jagsUI' (version 1.5.1; Kellner, 2019). Uninformative priors were used for all parameters and model convergence was assessed using the R-hat value and by visual examination of trace plots (Gelman et al., 2014).

To assess differences in prey group occupancy between core and edge zones, we compared two models for each prey group, one in which the occurrence of a group's members varied by zone and a second where their occurrence did not vary by zone (constant model). We selected the top-ranked model for each prey group by comparing the Deviance Information Criterion (DIC) scores of competing models. Prey occupancy probabilities were then derived from the top-ranked models. For

prey groups with multiple species, occupancy was defined as the probability that a site was occupied by at least one of the group's species.

#### 2.4. Clouded leopard density estimation

Spatially explicit capture-recapture analyses were used to estimate densities of clouded leopards using the 'secr' package (Efford, 2019) in program R (version 3.6.0; R Development Core Team, 2019). Clouded leopard individuals were identified based on their unique coat patterns (Fig. 2). Sex was identified based on the presence/absence of observable testicles and was included in our analyses as an individual covariate to account for heterogeneity in movements (Sollmann et al., 2011). Due to an uneven capture rate of left and right-flanks, we constructed two separate capture histories for each zone of disturbance (i.e., core-left, core-right, edge-left, and edge-right), selecting the capture histories with the most detections in each zone for analysis. In both zones, the right-flank capture histories possessed the most detections and were thus selected. Capture histories were defined using daily occasions starting from 0000 h and ending at 2359 h. To create a habitat mask, we applied a buffer of 11000 m around each camera-station, truncated at the reservoir's edge and the protected area's boundary where necessary. This buffer width was designated using the results of the 'secr' package's 'suggest.buffer' function.

We conducted multi-session analyses using the 'secr' R package, with capture histories from core and edge areas treated as separate sessions. AIC<sub>C</sub> scores and AIC<sub>C</sub> weights were used to determine the best-supported models. All models were fit using the full likelihood approach, with density varying by zone of disturbance. We varied density by zone in all models because no individuals were detected in both zones, indicating largely separate populations. We varied sigma ( $\sigma$ ) by sex in all models, as felids typically exhibit sex specific differences in home range sizes and movements (Sollmann et al., 2011). We modeled sex ratio ('pmix') as a function of zone.

Because we used bait, we modeled the baseline encounter probability parameter ( $g_0$ ) as a function of four different behavioral responses: learned response model ( $g_0 \sim b$ ; a global, permanent change in behavior after initial capture), site-specific learned response model ( $g_0 \sim bk$ ; a trap-specific, permanent change in behavior after initial capture), transient response model ( $g_0 \sim B$ ; a global, temporary change in behavior dependent on the previous capture), and site-specific transient response model ( $g_0 \sim Bk$ ; a trap-specific, temporary change in behavior dependent on the previous capture) (Efford, 2019). Finally, to test for an effect of prey availability on clouded leopard movements ( $\sigma$ ), we modeled  $\sigma$  as a function of zone. Due to high model uncertainty among our final top-ranked models ( $\Delta AIC_C < 2.00$ ), we used model averaging to estimate clouded leopard densities in each zone, using the "model.average" function in package 'secr' (Efford, 2019).

### 3. Results

In 5242 trap-days, we identified 21 complete clouded leopard individuals (i.e., both right and left flanks photographed), 6 right-flank only individuals, and 4 left-flank only individuals (Table 1). Thus, at least 27 clouded leopards were detected overall (21 complete + 6 right-only). The 4 left-flank only individuals were not considered in further analyses. Of the 27 individuals used in our analyses, 15 clouded leopards were identified in the core and 12 in the edge. No individuals were detected in both zones, indicating largely separate populations in each zone. The observed sex ratio (of complete individuals)



**Fig. 2.** Right-flank photographs of two different mainland clouded leopard (*Neofelis nebulosa*) individuals, photographed in southern Thailand's Khlong Saeng – Khao Sok Forest Complex, 2016–2017. Individuals were identified and distinguished based on unique cloud-like markings present on the species' coat.



**Table 1**

Summary of survey effort and mainland clouded leopard (*Neofelis nebulosa*) detections from southern Thailand's Khlong Saeng – Khao Sok Forest Complex. Trap-days are the number of days in which at least one of a station's three camera-traps remained operational.

Survey information	Core area	Edge area
Camera-trapping period	Feb–June 2016	Dec 2016–May 2017
Number of camera-trap stations	20	20
Trap Polygon	200 km <sup>2</sup>	297 km <sup>2</sup>
Total trap-days	2228	3014
Average distance between camera-traps	3516 m	3937 m
Number of daily sampling occasions	133	164
Notionally independent detections ( $\geq 30$ min)	33	31
Individuals with both flanks photographed	13	8
Individuals with only right-flanks photographed	2	4
Individuals with right-flank known	15	12
Individuals with only left-flanks photographed	2	2
Individuals with left-flank known	15	10
Number of individuals captured only once	14	8
Number of individuals recaptured	3	6
Sex composition (individuals with both flanks known)	7 ♂, 6 ♀, 0 unknown	6 ♂, 2 ♀, 0 unknown

was 1.2:1 (male:female) in the core and 3:1 in the edge (Table 1). At least 29 additional mammal species ( $\geq 1$  kg) were detected, of which 13 species are potential clouded leopard prey (Appendix 2).

### 3.1. Prey availability

Models with occupancy as a function of zone outperformed models with occupancy held constant, for four of six prey groups: muntjacs, wild boar, macaques, and small carnivores (Appendix 3). Estimates of occupancy were 56% higher in the core for muntjacs (core: 1.00, 95% CI 0.97–1.00; edge: 0.64, 95% CI 0.43–0.82) and 10% higher in the core for wild boar (core: 1.00, 95% CI 0.97–1.00; edge: 0.91, 95% CI 0.77–0.99), but 27% lower in the core for macaques (core: 0.63, 95% CI 0.44–0.80%; edge: 0.86, 95% CI 0.70–0.96) and 2% lower in the core for small carnivores (core: 0.66, 95% CI 0.48–0.81; edge: 0.67, 95% CI 0.50–0.82). However, only muntjac occupancy varied significantly between zones, with 95% credible intervals that did not overlap between zones (Fig. 3). Porcupine and mouse deer group occupancies did not vary by zone and were, overall, 0.22 (95% CI 0.11–0.36) and 0.44 (95% CI 0.30–0.59), respectively.

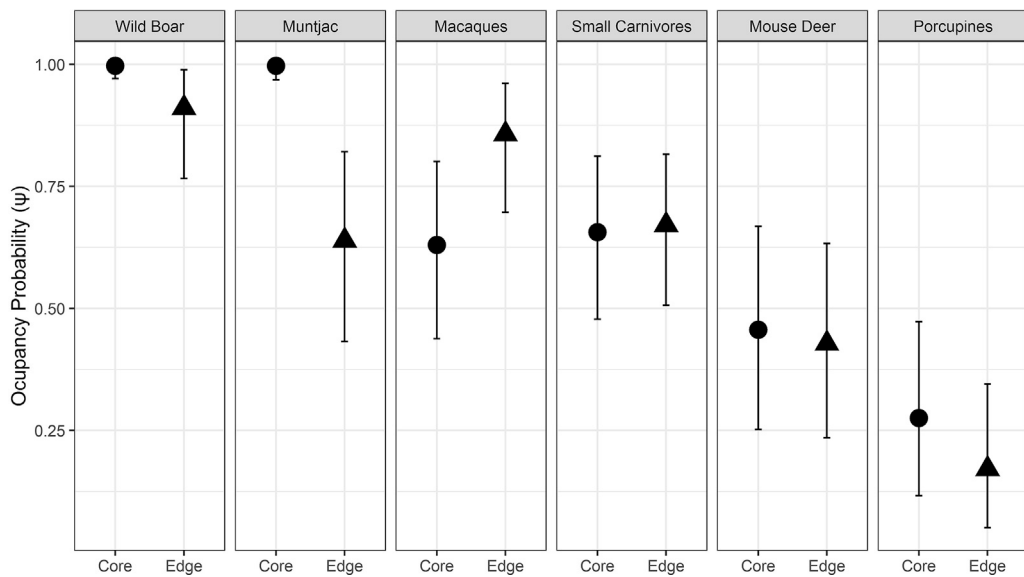
### 3.2. Clouded leopard density and movements

We compared five models examining the effects of different behavioral responses on baseline encounter probability ( $g_0$ ) and the effects of sex and zone on scale of movement ( $\sigma$ ) (Table 2). Two-top ranked models emerged with a cumulative AICc weight ( $w_i$ ) of 95% (Table 2). Model-averaged estimates of density from these two models indicate clouded leopard density was 62% higher in the core (5.06/100 km<sup>2</sup>; SE 1.64; 95% CI 2.75–9.41) compared to the edge (3.13/100 km<sup>2</sup>; SE 1.05; 95% CI 1.65–5.94).

Movement estimates of the two top-ranked models were similar. Based on our top-ranked model, movements ( $\sigma$ ) of male clouded leopards (3346 m; SE 509 m; 95% CI: 2487–4501 m) were 41% greater than those of female clouded leopards (2447 m; SE 447 m; 95% CI: 1716–3490 m). Estimates from our second top-ranked model indicate movements of male clouded leopards (3555 m; SE 574 m; 95% CI: 2595–4869 m) were 39% greater than movements of female clouded leopards (2558 m; SE 502 m; 95% CI: 1747–3745 m). The beta coefficient for sigma~zone using the model [D(zone)  $g_0(B)$   $\sigma(\text{sex} + \text{zone})$ ;  $w_i = 0.05$ ] suggested that zone of disturbance had little effect on clouded leopard movements (beta = -0.001; SE 0.26) once sex-specific differences in movements were accounted for. Estimates of male movements ranged from 3345 m (SE 544 m; 95% CI: 2436–4592 m) in the edge to 3349 m (SE 863 m; 95% CI 2038–5505 m) in the core, while estimates of female movements ranged from 2444 m (SE 714 m; 1395–4282 m) in the edge to 2448 m (SE 457 m; 1702–3519 m) in the core.

Common to both top-ranked models was the positive influence of a “transient” (temporary) behavioral response ( $B$  and  $B_k$ ) on  $g_0$ , indicating that for at least part of our study clouded leopards were generally “trap-happy” in response to our use of a non-reward bait. For the top-ranked model [D(zone)  $g_0(B)$   $\sigma(\text{sex})$ ;  $w_i = 0.48$ ], daily baseline encounter rates increased over 10-fold from 0.00452 (SE 0.00140; 95% CI 0.00248–0.00828) without a global behavioral response to 0.04680 (SE 0.02248; 95% CI 0.01796–0.11646) with one. Differences in encounter probabilities for the second top-ranked model, [D(zone)  $g_0(B_k)$   $\sigma(\text{sex})$ ;  $w_i = 0.47$ ], were even greater, ranging from 0.00453 (SE 0.00139; 95% CI 0.00247–0.00826) without a site-specific behavioral response to 0.11868 (SE 0.06639; 95% CI 0.03736–0.31843) with one.

Estimated sex ratios were similar for both top-ranked models, with 57% (SE 15%) of individuals in the core estimated to be female and 43% (SE 15%) male. This ratio was reversed in the edge, with 58% (SE 16%) male and 42% (SE 16%) female.



**Fig. 3.** Posterior mean occupancy probabilities and corresponding 95% Credible Intervals for six potential mainland clouded leopard (*Neofelis nebulosa*) prey groups, compared between two zones (core and edge) of southern Thailand's Khlong Saeng – Khao Sok Forest Complex, 2016–2017. This figure uses results from  $\psi(\text{zone}) p(\cdot)$  models (Appendix 3) for all prey groups.

**Table 2**

Model selection for mainland clouded leopard (*Neofelis nebulosa*) density using spatially-explicit capture-recapture. 'K' represents the number of estimated parameters.  $AIC_C$ ,  $\Delta AIC_C$ , and  $AIC_C$  weights ' $w_i$ ' provide a measure of relative support for each model.

Models	K	$AIC_C$	$\Delta AIC_C$	$w_i$
D(zone) g0(B) $\sigma(\text{sex})$	8	707.41	0.00	0.48
D(zone) g0(Bk) $\sigma(\text{sex})$	8	707.42	0.01	0.47
D(zone) g0(B) $\sigma(\text{sex} + \text{zone})$	9	712.00	4.59	0.05
D(zone) g0(bk) $\sigma(\text{sex})$	8	717.74	10.33	0.00
D(zone) g0(b) $\sigma(\text{sex})$	8	717.94	10.53	0.00

#### 4. Discussion

This study provides the first published density estimates for clouded leopards in Thailand and is one of the few studies to compare densities between sites with different prey availabilities and levels of poaching pressure. Clouded leopard density was notably higher in the less-disturbed core zone compared to the edge. The 62% difference in core and edge densities was not statistically significant, due to the low precision of density estimates caused by low recapture rates, but seems high enough to suggest a biologically significant difference in density between these two zones. Each zone has similar forest (both semi-evergreen), so habitat is not implicated in this difference. The notable distinction between these zones is in human access and poaching pressure, and in prey availability, with the core zone having significantly higher muntjac occupancy. Muntjacs (14–28 kg) are a potentially important prey species for clouded leopards because of their large body size relative to the size of a clouded leopard (11–23 kg)—a single muntjac would supply more food to a clouded leopard than any other available prey species except wild boar (which are also potentially more dangerous). Muntjacs are commonly hunted by humans in Thailand, with the meat eaten for subsistence as well as sold in local and urban markets (Tungtittiplakorn and Dearden, 2002; Steinmetz et al., 2006). The edge zone's relative accessibility and higher poaching rates likely resulted in the lower muntjac occupancy observed there. Wild boar and mouse deer are also commonly hunted in Thailand, but these species have high fecundity which renders them particularly resilient to poaching pressure (Lekagul and McNeely, 1977; Steinmetz et al., 2010); this might explain why occupancy rates of wild boar and mouse deer did not differ substantially between the core and the more heavily-hunted edge zone.

In Khlong Saeng, gun-hunting is the primary method of poaching. Although individual clouded leopards might be opportunistically shot when encountered by gun-hunters in the forest, such encounters are probably rare due to the cryptic nature of this species. Thus, we consider differences in prey availability to be a more likely explanation for the differences in clouded leopard density we observed. However, we note while muntjac occupancy varied significantly by zone, occupancies of other prey groups did not differ significantly. Thus, with the exception of muntjacs, overall prey availability appeared to be generally equivalent between zones. It is also notable that the edge zone's clouded leopard density of 3.13 individuals/

100 km<sup>2</sup>, although lower than the core, was not exceedingly low compared to published density estimates elsewhere (Table 3). This suggests overall prey availability in the edge, although relatively depauperate of muntjacs, was nonetheless sufficient to support a relatively high density of clouded leopards. Therefore, we posit that differences in core and edge densities are due to reduced exploitation competition with human poachers for muntjac in the core, rather than a shortage of prey in the edge. Furthermore, the apparent similarities in core and edge prey availability, with the exception of muntjacs, might also explain why clouded leopard movements ( $\sigma$ ) did not vary by zone (against our prediction) once sex-specific differences in movements were accounted for.

The correlation between clouded leopard density and the availability of large prey such as muntjacs is not consistent across existing studies and might be contingent on local conditions. Consistent with our study, Ngoprasert et al. (2012b) found a positive association between the distribution of clouded leopards and the photo-encounter rates of muntjac and wild boar across several protected areas in Thailand. In contrast, clouded leopard habitat use at two sites in Peninsular Malaysia was correlated with the photo-encounter rates of small prey, with little influence from larger prey such as muntjac (Mohamad et al., 2015). However, clouded leopards in the Mohamad et al. (2015) study coexisted with both tigers and leopards, two potential competitors that may influence the habitat use and prey selection of clouded leopards. Notably, Mohamad et al. (2015) found the density of clouded leopards to be significantly higher in the site with fewer tigers, despite less overall prey and more human disturbance, suggesting the distribution of clouded leopards might have actually been affected by tigers. Clouded leopards in Khlong Saeng, however, are not subject to such potential competition, as both tigers and leopards are locally extinct (or nearly so, for leopards). This might allow clouded leopards to more freely target larger-bodied prey species such as muntjac or even wild boar. Other competitively-subordinate felid species have undergone such competitive releases in diet. For example, ocelots (*Leopardus pardalis*) and pumas (*Puma concolor*) ate larger prey species in the absence of larger sympatric jaguars (*Panthera onca*) compared to sites where jaguars were present (Moreno et al., 2006).

Ultimately, we suspect both small and large prey are likely important for clouded leopards, with site-specific selection dependent on the relative availability of different prey, the presence of other sympatric large carnivores (i.e., niche partitioning), and habitat type (which may cause variation in the hunting success of different prey species) (Yarnell et al., 2013; Tablado et al., 2014; Moreira-Arce et al., 2015; Hayward et al., 2017). The size of clouded leopards (11–23 kg), as well as their sexual dimorphism in body mass, also suggests the dietary importance of both small and large prey. Clouded leopards, particularly males, approach or exceed a body mass of 15–20 kg, a threshold at which the diet of terrestrial carnivores is predicted to switch from small prey (<50% of predator mass) to large prey (>50% predator mass) (Carbone et al. 1999, 2007). Other carnivore species within this transitional weight range hunt both small and large prey (e.g., Gittleman, 1985; Carbone et al., 1999), and clouded leopards might be similar. In addition, the species' strong sexual dimorphism in body mass might result in sex-specific prey preferences among clouded leopards, with smaller females targeting smaller prey and larger males targeting larger prey. Although not yet studied in clouded leopards, such sex-specific differences in prey selection occur among other felids (e.g., cheetahs *Acinonyx jubatus*, Tambling et al., 2014; leopards *P. pardus*, Rostro-García et al., 2018). However, two important limitations of this study and others (e.g., Mohamad et al., 2015) in interpreting the effects of prey availability on clouded leopard behavior and density are the use of indirect data (i.e., prey indices from terrestrial camera-traps) and not accounting for arboreal prey abundance. Future studies should seek to estimate prey abundance or biomass directly and include arboreal prey as well.

#### 4.1. A regional comparison of clouded leopard density

We compared our estimates of clouded leopard density with other SECR-based density estimates in mainland Asia. Our estimates of 5.06 and 3.13 individuals per 100 km<sup>2</sup> in the core and edge, respectively, are comparable to or even higher than estimates from two sites in India (4.73/100 km<sup>2</sup>, Borah et al., 2014; 5.14/100 km<sup>2</sup>, Singh and Macdonald, 2017), two sites in Myanmar (0.60/100 km<sup>2</sup> and 3.05/100 km<sup>2</sup>, Naing et al., 2017), two sites in Peninsular Malaysia (1.83/100 km<sup>2</sup> and 3.46/

**Table 3**

Comparison of density estimates (D; individual/100 km<sup>2</sup>), standard errors (SE), and coefficients of variation (CV; SE/D) from published studies of mainland clouded leopards (*Neofelis nebulosa*) based on spatially-explicit capture-recapture analysis. Standard deviations and corresponding coefficients of variation (SD/D) are included for Bayesian estimates and denoted with asterisks.

Study	D	SE	CV	Location	Method
This study	5.06	1.64	0.32	(Core) Khlong Saeng – Khao Sok Forest Complex, Thailand	MLE
	3.13	1.05	0.34	(Edge) Khlong Saeng – Khao Sok Forest Complex, Thailand	MLE
Borah et al. (2014)	4.73	1.43	0.30	Manas National Park, India	MLE
Mohamad et al. (2015)	3.46	1.00	0.29	Temengor, Peninsular Malaysia	MLE
	1.83	0.61	0.33	Belum, Peninsular Malaysia	MLE
Naing et al. (2017)	0.60	0.24*	0.40*	Nam Pa Gon, Htamanthi Wildlife Sanctuary, Myanmar	Bayesian
	3.05	1.03*	0.34*	Nam E Zu, Htamanthi Wildlife Sanctuary, Myanmar	Bayesian
Singh and Macdonald (2017)	5.14	1.80*	0.35*	Dampa Wildlife Reserve, India	Bayesian
Penjor et al. (2018)	0.30	0.12	0.40	Bhutan	MLE
	0.40	0.10*	0.25*	Bhutan	Bayesian

MLE: Maximum Likelihood Estimation.

100 km<sup>2</sup>; Mohamad et al., 2015) and Bhutan (0.40/100 km<sup>2</sup>; Penjor et al., 2018) (Table 3). Variation in clouded leopard densities could be caused by competition with leopards and tigers, species which might affect clouded leopard behavior (e.g., reducing capture probability by increasing arboreality or decreasing trail usage), reduce their access to large prey, or suppress their density. Ngoprasert et al. (2012b), for example, identified a possible negative relationship between clouded leopards and leopards when comparing their occurrence across several protected areas in Thailand. Notably, Khlong Saeng lost its tigers decades ago, and leopards appear to have been recently extirpated; these drastic changes to the carnivore community may have contributed to the relatively high clouded leopard densities we observed compared to other studies.

Focused studies on potential interactions between clouded leopards and larger sympatric felids are lacking, but four existing studies suggest that clouded leopards tend to be more abundant where tigers are scarce. For example, the density of clouded leopards in selectively logged Temengor Forest Reserve (Malaysia) was 3.46/100 km<sup>2</sup>, nearly double that compared to nearby Royal Belum State Park despite lower prey availability and more human disturbance in Temengor; notably, tigers were 3 times more abundant in Royal Belum (Mohamad et al., 2015; Rayan and Linkie, 2015). Leopards were also more abundant in the site with fewer tigers (Rayan and Linkie, 2016). Likewise, clouded leopard density in Manas National Park (India) was 4.73/100 km<sup>2</sup>, the third-highest on record, at a time when tigers were nearly extirpated in Manas (Borah et al., 2014; J. Borah, pers. comm.). Leopard density, like that of clouded leopards, was also relatively high in Manas at the time (Borah et al., 2014). In Myanmar, clouded leopard density was over five times higher (3.05/100 km<sup>2</sup>) at a disturbed site where tigers were relatively rare, compared to a less disturbed site with more tigers, despite similar habitats and similar small and medium-sized prey availability (Naing et al., 2017). Leopards were rare at both sites. Finally, Dampas Tiger Reserve in India, where both tigers and leopards have been extirpated, supports the highest clouded leopard density so far documented (Singh and Macdonald, 2017). Though this apparent pattern of negative correlations between densities of clouded leopards and tigers does not prove cause and effect, it does suggest some sort of competitive effect that warrants future study. This is particularly important if tigers influence the detectability of clouded leopards, in which case surveys in areas with tigers might be observing only a subset of the clouded leopard population and possibly underestimating density. Focused research on clouded leopard behavior under varying tiger densities would be needed to explore this subject further and may prove informative for future conservation efforts.

Our study provides novel insights about the population status of mainland clouded leopards, their behavioral ecology, and response to human disturbance. Our study also highlights the potential importance of the Khlong Saeng – Khao Sok Forest Complex as a conservation stronghold for clouded leopards in southern Thailand. With one of the highest density estimates on record, the forest complex might serve as a potential source population. More research is needed to understand the long-term viability of this population, its connectivity to nearby forests, and the influence of prey availability and poaching on population dynamics.

### Declaration of competing interest

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

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### Appendix 1. Summary of criminal cases from the Khlong Saeng – Khao Sok Forest Complex, 2009–2017. Cases include poaching, logging, and non-timber forest products (NTFP) collection

Year	Core		Edge	
	Poaching	Logging/NTFP	Poaching	Logging/NTFP
2017	0	0	1	0
2016	0	0	3	2
2015	2	0	3	4
2014	4	0	6	4
2013	3	0	1	3
2012	2	1	5	2



(continued)

Year	Core		Edge	
	Poaching	Logging/NTFP	Poaching	Logging/NTFP
2011	0	0	2	5
2010	1	1	6	8
2009	0	0	6	9
Total	12	2	33	37

Source: Department of National Parks, Wildlife and Plant Conservation, Thailand. <http://portal.dnp.go.th/Content?contentId=2134>

## Appendix 2. Mammal species detected by camera-traps within southern Thailand's Khlong Saeng – Khao Sok Forest Complex, 2016–2017. IUCN Red List status\* and photo-encounter rates\*\* within both the core and edge areas included for each species

Common Name	Scientific Name	IUCN*	Core**	Edge**
Dusky Langur	<i>Trachypithecus obscurus</i>	NT	0.09	0.03
Southern Pig-tailed Macaque	<i>Macaca nemestrina</i>	VU	0.40	0.10
Stump-tailed Macaque	<i>Macaca arctoides</i>	VU	1.17	1.89
Asiatic Black Bear	<i>Ursus thibetanus</i>	VU	6.55	3.28
Sun Bear	<i>Helarctos malayanus</i>	VU	9.52	6.93
Yellow-throated Marten	<i>Martes flavigula</i>	LC	0.04	0.13
Banded Civet	<i>Hemigalus derbyanus</i>	NT	0.00	0.17
Binturong	<i>Arctictis binturong</i>	VU	0.76	0.36
Common Palm Civet	<i>Paradoxurus hermaphroditus</i>	LC	0.09	0.27
Large Indian Civet	<i>Viverra zibetha</i>	LC	0.00	0.03
Masked Palm Civet	<i>Paguma lavarta</i>	LC	0.58	0.40
Crab-eating Mongoose	<i>Herpestes urva</i>	LC	0.27	0.10
Asiatic Golden Cat	<i>Catopuma temminckii</i>	NT	1.08	0.56
Mainland clouded Leopard	<i>Neofelis nebulosa</i>	VU	1.48	1.03
Leopard Cat	<i>Prionailurus bengalensis</i>	LC	0.04	0.17
Marbled Cat	<i>Pardofelis marmorata</i>	NT	0.00	0.03
Sunda Pangolin	<i>Manis javanica</i>	CR	0.04	0.00
Asian Elephant	<i>Elephas maximus</i>	EN	1.44	0.33
Malayan Tapir	<i>Tapirus indicus</i>	EN	2.33	2.12
Wild Boar	<i>Sus scrofa</i>	LC	24.51	14.07
Mouse Deer spp.	<i>Tragulus</i> spp.	–	0.90	1.72
(Greater Mouse Deer)	<i>T. napu</i>	LC	–	–
(Lesser Mouse Deer)	<i>T. kanchil</i>	LC	–	–
Muntjac spp.	<i>Muntiacus</i> spp.	–	4.67	1.96
(Northern Red Muntjac)	<i>M. vaginalis</i>	LC	–	–
(Fea's Muntjac)	<i>M. feae</i>	DD	–	–
Sambar	<i>Rusa unicolor</i>	VU	3.90	0.43
Chinese Serow	<i>Capricornis milneedwardsii</i>	NT	0.58	1.03
Gaur	<i>Bos gaurus</i>	VU	1.75	0.86
Grey-bellied Squirrel	<i>Callosciurus caniceps</i>	LC	0.00	0.07
Indomalayan Bamboo Rat	<i>Rhizomys sumatrensis</i>	LC	0.13	0.00
Asiatic Brush-tailed Porcupine	<i>Atherurus macrourus</i>	LC	0.40	0.20
Malayan Porcupine	<i>Hystrix brachyura</i>	LC	3.32	2.55

\*DD-Data Deficient; LC-Least Concern; NT-Near Threatened; VU-Vulnerable; EN-Endangered; CR-Critically Endangered.

\*\*Notionally independent detections/100 camera-trap trap-days. Detections were considered notionally independent if the time between photographs  $\geq 30$  min (O'Brien et al., 2003). Trap-days defined as 24 h periods between 0000 and 2359 where at least one camera-trap was operating at a camera-station.

## Appendix 3. Occupancy model selection for potential mainland clouded leopard (*Neofelis nebulosa*) prey species in southern Thailand's Khlong Saeng – Khao Sok Forest Complex, 2016–2017. Prey groups were analyzed separately and modeled using either single-species or multi-species occupancy models depending on the number of species within a group. For multi-species models with $\psi(\text{zone})$ , we modeled the occupancy of all species as a function of zone

Model	Model Type	DIC	$\Delta$ DIC
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Model	Model Type	DIC	ΔDIC
Muntjac spp.*			
$\psi(\text{zone})$ p(.)	Single-species	204.77	0.00
$\psi(\cdot)$ p(.)	Single-species	215.84	11.07
Wild boar			
$\psi(\text{zone})$ p(.)	Single-species	587.92	0.00
$\psi(\cdot)$ p(.)	Single-species	589.34	1.42
Macaques			
$\psi(\text{zone})$ p(.)	Multi-species	222.57	0.00
$\psi(\cdot)$ p(.)	Multi-species	225.25	2.68
Small carnivores			
$\psi(\text{zone})$ p(.)	Multi-species	301.69	0.00
$\psi(\cdot)$ p(.)	Multi-species	308.32	6.63
Mouse deer			
$\psi(\cdot)$ p(.)	Multi-species	170.18	0.00
$\psi(\text{zone})$ p(.)	Multi-species	171.62	1.44
Porcupines			
$\psi(\cdot)$ p(.)	Multi-species	94.39	0.00
$\psi(\text{zone})$ p(.)	Multi-species	96.61	2.22

\*Fea's muntjac (*Muntiacus feae*) and northern red muntjac (*M. vaginalis*) detections were aggregated due to uncertainties in identification.

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