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ARTICLE

ESTIMATING LEOPARD CAT PRIONAILURUS BENGALENSIS KERR, 1792 (CARNIVORA: FELIDAE) DENSITY IN A DEGRADED TROPICAL FOREST FRAGMENT IN NORTHEASTERN THAILAND

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ESTIMATING LEOPARD CAT *PRIONAILURUS BENGALENSIS* KERR, 1792 (CARNIVORA: FELIDAE) DENSITY IN A DEGRADED TROPICAL FOREST FRAGMENT IN NORTHEASTERN THAILAND

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Abstract: The Leopard Cat *Prionailurus bengalensis* is thought to be Asia's most abundant wild cat. Yet, the species' status is poorly known due to a lack of rigorous population estimates. Based on the few studies available, Leopard Cats appear to be more abundant in degraded forests, potentially due to increased prey availability. We conducted camera trap surveys, rodent live-trapping, and spatially-explicit capture-recapture analyses to estimate the density of Leopard Cats within a degraded tropical forest fragment (148km²) in northeastern Thailand. A total effort of 12,615 camera trap nights across 65km² of trapping area resulted in at least 25 uniquely identified individuals. Average rodent biomass (the main prey of Leopard Cats) was highest in the dry evergreen forest (469.0g/ha), followed by dry dipterocarp forest (287.5g/ha) and reforested areas (174.2g/ha). Accordingly, Leopard Cat densities were highest in the dry evergreen forest with 21.42 individuals/100km², followed by the reforested areas with 7.9 individuals/100km². Only two detections came from the dry dipterocarp forest despite both an extensive survey effort (4,069 trap nights) and available prey. Although the dipterocarp supported the second highest average rodent biomass, it lacked a key prey species, *Maxomys surifer*, possibly explaining low encounter rates in that habitat. Our results provide important baseline information concerning the population status of Leopard Cat in southeastern Asia. Further, our findings corroborate with other studies that found a tolerance among Leopard Cats for degraded forests, highlighting the potential for forest fragments to serve as long-term conservation areas for the species.

Keywords: Camera trapping, Least Concern, predator-prey, prey availability, rodent biomass, Sakaerat Biosphere Reserve, southeastern Asia, spatially-explicit capture-recapture.

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Author contribution: WJP, DN, RS, TS conceived the ideas and designed field methodology; WJP collected the data; WJP, DN analyzed the data; WJP, DN, RS, TS contributed critically to the drafts and all authors gave final approval for publication.

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INTRODUCTION

When confronted with a lack of rigorous population estimates, status assessments such as the IUCN Red List of Threatened Species must rely on expert opinion of trends in population abundance or geographic range (Mace et al. 2008). This, however, can be problematic given both the subjective nature of expert opinion (Regan et al. 2005) as well as the wide variation in population dynamics and threats faced across a species range. The Leopard Cat Prionailurus bengalensis, for example, is thought to be the most abundant small cat species in Asia due to its wide distribution and supposed tolerance towards human-modified landscapes (Nowell & Jackson 1996; Macdonald et al. 2010; Ross et al. 2010). Yet, little is known regarding Leopard Cat population status in most parts of its range. Furthermore, recent studies suggest that Leopard Cat populations, in at least some areas, are being adversely affected by habitat loss, fragmentation, and poaching (e.g., Seto et al. 2012; Coudrat et al. 2014a,b; Willcox et al. 2014). As a result, the Leopard Cat may be threatened in many areas at a local scale, despite its global status on the IUCN Red List as Least Concern (Ross et al. 2010).

Camera trapping is an effective approach for estimating the density of uniquely marked animals such as Leopard Cats (Balme et al. 2009; Royle et al. 2013). However, despite widespread use of camera traps throughout the Leopard Cat's extensive geographic range, estimates of density are available from just a few sites in India and Malaysian Borneo (Bashir et al. 2013; Mohamed et al. 2013; Selvan et al. 2014; Srivathsa et al. 2015). This paucity of data may be due to multiple reasons such as 1) a lack of interest or incentive among researchers towards studying a species listed as Least Concern by the IUCN or 2) an inherent bias in survey effort towards other species and habitats not utilized by Leopard Cats. Moreover, Marshall et al. (2016) clearly demonstrated tropical research to be heavily biased towards large, charismatic, and threatened species as well as towards large, intact, primary forests. This bias is relevant given that several studies from primary forests found Leopard Cats to be among the least recorded Asian felids (e.g., Ross et al. 2010; McCarthy et al. 2015). Furthermore, studies by Mohamed et al. (2013) and Srivathsa et al. (2015) found Leopard Cat densities to be higher in more degraded habitats, which tend to be ignored by researchers. Despite their high tolerance for degraded habitats, telemetry studies suggest that Leopard Cats are still forest-dependent to some extent (Rajaratnam et al. 2007) and may even avoid large

artificial open areas such as agriculture lands and human settlements (Chen et al. 2016).

An association between Leopard Cats and degraded habitats may reflect the species diet, which consists predominantly of murid rodents (e.g., Yasuma 1981; Rabinowitz 1990; Grassman 1998; Grassman 2000; Grassman et al. 2005; Rajaratnam et al. 2007). Indeed, rodent biomass is often elevated in degraded habitats owing to either increased resource availability (e.g., invertebrates), reduced predation pressure, or both (Lambert et al. 2006; Wells et al. 2007; Pimsai et al. 2014). Yet, in most studies on Leopard Cat habitat use and diet, prey distribution and abundance were not measured, despite these apparent associations between predator, prey, and habitat. Of the studies that did measure prey distribution and abundance, several indicated that Leopard Cats may preferentially select habitats based on the availability of a specific key prey species, rather than overall prey abundance (Yasuma 1981; Rabinowitz 1990; Rajaratnam et al. 2007).

In this study, we estimated Leopard Cat density using spatially-explicit capture-recapture models applied to a camera trapping dataset from a degraded tropical forest fragment in northeastern Thailand. Our study spanned periods of rodent abundance and scarcity in three forest types, allowing us to observe the response of Leopard Cats to both spatial and temporal changes in resource availability. We made two predictions. First, Leopard Cat density should be highest in the forest type with the highest average rodent biomass (g/ha), as forest types with more food should support higher Leopard Cat densities compared to forest types with less food. Second, Leopard Cat movements (sigma parameter) should be larger when and where resources are scarce, compared to when and where they are abundant. This pattern would reflect possible increases in ranging behaviour in response to low resource availability (Fuller & Sievert 2001). We then compared overall density at our site to density estimates from other sites throughout the species range.

STUDY AREA

Established in 1977, the Sakaerat Biosphere Reserve (hereafter Sakaerat) in northeastern Thailand (14.510°N & 101.930°E) covers 148km^2 of fragmented forest with an elevation range of 280-762 m (Fig. 1). Historically, the areas comprising Sakaerat's present-day reserved forest underwent periods of extensive deforestation and conversion to agriculture (the 1950s–1970s), followed

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Figure 1. Sakaerat Biosphere Reserve in Thailand, including three dominant habitat types, camera trap locations, rodent live-trapping locations, and Highway 304.

by state-run reforestation efforts using non-native tree species (1977 onwards). This process of deforestation and reforestation resulted in the fragmentation and isolation of Sakaerat from nearby forests (including Dong Phayayen-Khao Yai forest complex) and greatly altered the reserve's current forest structure, with no primary forest remaining (Kamo et al. 2002; TISTR 2018).

Dominant forest types today include secondary dry evergreen forest (hereafter evergreen; 54%), secondary dry dipterocarp forest (hereafter dipterocarp; 11%), and reforested areas (33%) which include secondary evergreen regrowth and mixed acacia (*Acacia* spp.) and eucalyptus (*Eucalyptus* spp.) forest plantations (Fig. 1; Ashton et al. 2014). Sakaerat has a seasonal climate with a dry season starting from November to April and a wet season from May to October. The average annual precipitation is 1,071mm, while the average annual temperature is 26.1°C (TISTR 2018).

MATERIALS AND METHODS

Camera trap surveys

We deployed 60 camera traps (Scout Guard SG565) spaced 1km apart in three forest types (evergreen: 28 camera traps; dipterocarp: 16 camera traps; reforested areas: 16 camera traps) from mid-January 2017 through October 2017 (Fig. 1). One camera trap was deployed per station. Camera traps were attached to trees approximately 45cm above the ground and 3m from a target zone, which was lured with fish oil scent. We visited camera traps once per month to replace batteries, memory cards, and the scent lure. We calculated trapping effort by summing the number of trap nights (24h-periods starting from 00.00h and ending at 23.59h), in which camera traps were both active and functioning.

Rodent biomass estimation

We sampled terrestrial rodents during four periods (February–March; April–May; July–August; September– October) in 2017 at 15 sites (seven sites in evergreen, four in dipterocarp, and four in reforested areas) using Sherman live traps (7.62cmx8.89cmx22.86cm). At each site, we arranged 25 traps on the ground in a 5x5 grid with 20m spacing between traps and used peanut butter as bait. Each session consisted of seven consecutive trap nights at one site, with sites being visited once per two-month period (60 sessions total). Captured animals were identified to species, weighed, uniquely marked with an ear tag (mouse ear-tag - style 1005-1), and then released at their capture sites. Rodent live-trapping protocol was approved by King Mongkut's University of Technology Thonburi's Animal Care and Use Committee and permitted by Thailand's Department of National Parks, Wildlife and Plant Conservation.

To estimate the biomass of rodents, we first estimated density (D) using the 'secr' package (Efford 2018) in program R (version 3.42; R Development Core Team, 2016). Due to the limited number of captures and recaptures at some sites, we pooled all species and sites from the same forest type and sampling period for analysis, with each site designated as a separate session. Data from different two-month sampling periods were analyzed separately. Multi-session analyses were then conducted whereby the capture parameters g0 (capture probability when the distance between an animal's activity center and the trap is zero) and sigma (σ ; a scaling parameter reflecting animal movement) were shared among sessions. To account for potential bias in our small mammal capture-probabilities introduced by "trap-happy" or "trap-shy" individuals, we incorporated various behavioral responses into our models (Otis et al. 1978; Efford 2018). Models tested included a constant model [D(session) g0(.) σ (.)], learned response model [D(session) g0(b) $\sigma(.)$; "trap-happy"], site-specific learned response model [D(session) g0(bk) $\sigma(.)$; trapspecific "trap-happy"], transient response model $[D(session) gO(B) \sigma(.);$ "trap-shy"], and site-specific transient response model [D(session) g0(Bk) $\sigma(.)$; trapspecific "trap-shy"]. Session-specific density estimates were then derived using the best-supported model as determined by AIC_c scores and AIC_c weights (Burnham & Anderson 2002).

Session-specific density estimates were then multiplied by the session's corresponding mean individual body mass to obtain session-specific estimates of rodent biomass (Chutipong et al. 2017). Session-specific rodent biomass estimates were then assigned as a covariate to the nearest four camera trap stations within the same habitat type for use in estimating Leopard Cat density.

Leopard Cat density estimation

Spatially-explicit capture-recapture analyses were used to estimate Leopard Cat densities (Efford 2018) based on each animal's unique spot patterns observed



Image 1. A diurnal Leopard Cat Prionailurus bengalensis investigating the fish oil scent lure placed at the centre of a camera trap's target zone within the dry evergreen forest of Sakaerat Biosphere Reserve, northeastern Thailand.

in camera trap images (Image 1). Because Leopard Cats are patterned asymmetrically, there is a possibility of photographing what is known as "partial identities" or individuals known from only a single flank. To include these "partial" individuals into the analyses, researchers typically analyze left and right flanks separately or discard the flank with the least detections (e.g., Wang & Macdonald 2009; Kalle et al. 2011; Srivathsa et al. 2015). These approaches, however, result in a loss of precision and the potential introduction of bias (Meredith 2017). To avoid this, we used a new method that combines data from both flanks into the same analysis, modelling each flank as a separate 'session' and estimating shared values for D, g0, and σ across sessions under the assumption that the latent ("true") density and capture probabilities of both flanks are equal (Meredith 2017).

After identifying individuals, we generated capture histories using daily occasions starting from 00.00h and ending at 23.59h. Capture histories were then split into different sessions based on the period of resource availability (i.e., high or low rodent biomass), habitat type (i.e., evergreen or reforested area), and flank (i.e., left or right). A mask (buffer=1500m; designated using the 'suggest.buffer' function) was also applied around each station, limited by the study area's boundary. We then conducted multi-session analyses, comparing a constant model [D(.) $gO(.) \sigma(.)$] to models where D, gO, and σ parameters varied by the season of resource availability (high rodent biomass and low rodent biomass; termed "season") and habitat type (evergreen and reforested area; termed "habitat"). In addition to these session-covariates, we also modelled the gO parameter using the trap-covariates "rodent biomass" which corresponds to the actual rodent biomass (g/ha) from the nearest rodent live-trapping site (see Rodent biomass estimation) and behavioral responses (e.g.,

trap-happy or trap-shy), using covariates "b", "bk", "B", and "Bk". Sigma (σ) was additionally modelled by the trap covariate "rodent biomass".

We performed our model selection in three steps using AIC_c scores and AIC_c weights to determine the bestsupported model (Burnham & Anderson 2002). First, we modelled all g0 covariates individually, while leaving D and σ constant. Second, any individual g0 covariates performing better than the constant model [g0(.)] were then modelled together using all possible combinations. The top-ranked covariate combinations ($\Delta AIC_c < 6.0$) from this second step were then considered "candidate covariate combinations". These two steps were then repeated for the D and σ parameters. Finally, we modelled D, g0, and o parameters using all combinations of D, g0, and σ "candidate covariate combinations". Due to our limited sample size, we restricted each model to a maximum of two covariates. All models were fit using the full likelihood approach.

RESULTS

In 12,615 camera trap nights, we obtained 115 images from 59 detections of Leopard Cats, of which 50 detections contained images that could be used to identify individuals (Table 1). Due to the species small body size, we could not identify the sex of the individuals. During the period of low rodent biomass, 14 left-flank individuals (12 in evergreen, two in reforested) and 13 right-flank individuals (12 in evergreen, one in reforested) were detected. Ten left-flank individuals (five in evergreen and five in reforested) and 11 right-flank individuals (six in evergreen and five in reforested) were detected during the period of high rodent biomass. Two left-flank individuals were detected in the dipterocarp

Table 1. Summary of Leopard Cat images by period of rodent biomass from Sakaerat Biosphere Reserve, northeastern Thailand. "Identifiable detections" refers to the number of Leopard Cat detections that contain images that are usable for individual identification. "Partial individuals" corresponds to the number of individuals that only had a single flank photographed (either right or left). "Complete individuals" corresponds to the number of individuals that only had a single flank photographed (either right or left). "Complete individuals" corresponds to the number of individuals that only had a single flank photographed. Dry evergreen forest: DEF; reforested areas: RFA; dry dipterocarp forest: DDF.

Survey Information	Low rodent biomass				High rodent biomass			
	Total	DEF	RFA	DDF	Total	DEF	RFA	DDF
Period	January–May 2017				June–October 2017			
Camera stations	58	28	14	16	58	28	14	16
Survey area	65km²	34km ²	15km²	16km²	65km²	34km ²	15km ²	16km²
Trap nights	7,193	3,726	1,341	2,126	5,422	2,136	1,349	1,937
Identifiable detections	25	22	3	0	25	13	10	2
Partial individuals (right-flank)	7	6	1	0	10	6	4	0
Partial individuals (left-flank)	7	5	2	0	11	5	4	2
Complete individuals (both flanks)	7	7	0	0	1	0	1	0

during the period of high rodent biomass. Because of our low sample size in the dipterocarp, we did not estimate Leopard Cat density in that habitat type.

Rodent biomass

In total, we conducted 10,500 small mammal trap nights, during which we captured 297 unique individuals of at least six rodent species (Table 2). Average density in the evergreen was highest in September-October (mean=7.3 individuals/ha; range of site-specific densities: 5.3-10.5 individuals/ha) and lowest in April–May (mean=1.3 individuals/ha; range: 0.4–1.7 individuals/ha). In the dipterocarp, average density was highest in July–August (mean=13.1 individuals/ha; range of site-specific densities: 0 individuals captured-38.6 individuals/ha) and lowest in April–May (mean=2.2 individuals/ha; range: 0 individuals captured-3.4 individuals/ha). In the reforested areas, the average density was highest in September–October (mean=5.2 individuals/ha; range of site-specific densities: 3.3-6.6 individuals/ha) and lowest in April–May (0 individuals captured).

Average rodent biomass was consistently highest in

the evergreen (mean=469.0 g/ha) throughout our study, followed by the dipterocarp (mean=287.5g/ha) and reforestation areas (mean=174.2 g/ha; Fig. 2). Seasonally, overall average rodent biomass was 3.6 times higher during the rainy season (July–October; mean=527.5g/ ha) compared to the dry season (February–May; mean=145.6g/ha). Overall rodent biomass peaked in the months of September–October (mean=763.8g/ha), especially in the evergreen (mean=995.0g/ha). April– May had the lowest overall rodent biomass (mean 91.8g/ ha), especially in the reforested areas (0 captures). As such, February–May was considered the period of low rodent biomass for all habitats and July–October was considered the period of high rodent biomass (Fig. 2).

Leopard Cat density

Our two top-ranked models based on AIC_c and AIC_c weights included D(.) g0(*b*) σ (*habitat*) (43% AIC_cw_i ; Table 3) and D(*habitat*) g0(*b*) σ (.) (20% AIC_cw_i ; Table 3). According to D(.) g0(*b*) σ (*habitat*), the Leopard Cat density within Sakaerat (excluding dipterocarp) was 17.7 individuals/100km² (SE 3.9; 95% CI 11.5–27.2; Table 4). The movement parameter, sigma (σ), was 480.2m



Dipterocarp Evergreen Reforested

Figure 2. Rodent biomass by habitat and bimonthly period. The period of high rodent biomass corresponds with July–August and September– October, while the period of low rodent biomass corresponds with February–March and April–May.

Table 2. Summary of small mammal live-trapping results including trap nights by habitat, the number of unique individuals captured by both habitat and species, and the average individual body mass by species. Live-trapping data from Sakaerat Biosphere Reserve, northeastern Thailand, 2017.

Survey information	Overall	Dry dipterocarp	Dry evergreen	Reforested areas	Average mass
Trap nights	10,500	2,800	4,900	2,800	-
Total capture events	297	137	133	27	-
Maxomys surifer	162	6	133	23	132.3g/indiv SE 2.0
Mus spp.	118	116	0	2	17.4g/indiv SE 0.5
Tupaia belangeri	10	10	0	0	177.6g/indiv SE 14.6
Menetes bermorei	4	4	0	0	198.3g/indiv SE 24.0
Crocidura attenuata	2	0	0	2	9.5g/indiv SE 0.5
Rattus rattus	1	1	0	0	79g/indiv

Table 3. Model selection for Leopard Cat density using spatially-explicit capture-recapture. 'K' represents the number of estimated parameters. AIC_c, Δ AIC_c, and AIC_c weights 'w' provide a measure of relative support for each model. Only models with a cumulative w <0.95 are included. For all models, see Appendix B.

Models	к	AIC _c	ΔAIC _c	w,
D(.) g0(b) sigma(habitat)	5	961.17	0.00	0.43
D(habitat) g0(b) sigma(.)	5	962.69	1.52	0.20
D(.) g0(.) sigma(habitat)	4	963.66	2.49	0.12
D(.) g0(habitat) sigma(habitat)	5	964.69	3.52	0.07
D(habitat) g0(.) sigma(habitat)	5	965.94	4.77	0.04
D(habitat) g0(.) sigma(.)	4	966.12	4.94	0.04
D(.) g0(habitat + bk) sigma(.)	5	966.30	5.13	0.03

(SE 98.6; 95% CI 322.1–715.9) in the evergreen and 236.2m (SE 53.1; 95% CI 152.8–365.1) in the reforested areas. The capture parameter g0 was 0.009 (SE 0.004) when b=0 and 0.002 (SE 0.0007) when b=1. Based on our second top-ranked model, D(*habitat*) g0(b) σ (.) Leopard Cat density was 21.2 individuals/100km² (SE 5.3; 95% CI 13.1–34.3; Table 3) in the evergreen and 7.9 individuals/100km² (SE 2.7; 95% CI 4.1–15.0; Table 3) in the reforested areas. Sigma (σ) was 476.0m (SE 93.4; 95% CI 325.2–696.7). g0 was 0.007 (SE 0.003) when b=0 and 0.001 (SE 0.0006) when b=1.

DISCUSSION

Our study is among the first to simultaneously conduct camera trapping and rodent live-trapping to assess the relationship between small wild cat density and prey biomass. Specifically, we estimated Leopard Cat density and examined the influence of rodent biomass and forest type on the species density and movements in a degraded tropical forest fragment. Contrary to our predictions, top-ranked models did not indicate a direct effect of rodent biomass or season on Leopard Cat density or movements (Table 3; Appendix B). This result could have several explanations. First, although we found major differences in rodent biomass between seasons and within habitat types, rodents were nonetheless always available throughout the year and the differences may not have been biologically significant enough to warrant detectable changes in Leopard Cat behavior. Second, although dietary studies indicate Leopard Cats predominantly eat murid rodents, the species also consumes other prey items including birds, reptiles, amphibians, and invertebrates (Grassman 1998; Grassman 2000; Grassman et al. 2005; Rajaratnam et al. 2007). The availability of such alternative prey, which we did not sample, may have mitigated the influence of rodent biomass on Leopard Cat density and behavior.

Our raw data, though, do suggest that seasonal differences in rodent biomass may influence Leopard Cat capture probability. For example, during the low rodent period, we obtained seven recaptures, five of which were relocations (i.e., recaptures at different

Table 4. Comparison of density estimates (D; individual/100km²), standard errors (SE), and coefficient of variation (CV) from our study and other studies of Leopard Cats using both maximum likelihood (MLE) and Bayesian spatially-explicit capture-recapture. For this study, density estimates come from two models: ^aD(.) g0(b) σ (habitat) and ^bD(habitat) g0(b) σ (.). ^cStandard deviation (SD) and ^dcoefficient of variation (CV) are included for Bayesian estimates.

Study	D	SE	сv	Location
This study	17.7ª	3.9	0.22	Overall, Sakaerat Biosphere Reserve, Thailand
	21.2 ^b	5.3	0.25	Semi-evergreen forest, Sakaerat Biosphere Reserve, Thailand
	7.9⁵	2.7	0.34	Artificially reforested areas, Sakaerat Biosphere Reserve, Thailand
Srivathsa et al. 2015	10.5	3.0°	0.29 ^d	Semi-evergreen and moist deciduous forest, Bhadra Tiger Reserve, India
	4.5	1.3°	0.29 ^d	Various habitats, Biligiri Rangaswamy Temple Tiger Reserve, India
Selvan et al. 2014	2.9	0.2	0.07	Wet evergreen forest, Pakke Tiger Reserve, India
Mohamed et al. 2013	12.4	1.6	0.13	Mixed dipterocarp forest, Tangkulap-Pinangah Forest Reserve, Malaysian Borneo
	16.5	2.0	0.12	Mixed dipterocarp forest, Segaliud Lokan Forest Reserve, Malaysian Borneo
	9.6	1.7	0.18	Mixed dipterocarp forest, Deramakot Forest Reserve, Malaysian Borneo
Bashir et al. 2013	17.0	5.3	0.31	Temperate broadleaf forest, Khangchendzonga Biosphere Reserve, India

camera locations). By contrast, during the high rodent period, there were only four recaptures, one of which was a relocation. We hypothesize that this reflects Leopard Cats being easier to capture during the period of low prey biomass, due to being more receptive to our scent lure and having larger home ranges, both of which would result in higher capture probabilities.

Our top-ranked model, D(.) $gO(b) \sigma(habitat)$, suggests that Leopard Cat movement was lower in reforested areas compared to the evergreen forest. Because reforested areas supported lower rodent biomass compared to the evergreen, this finding is contrary to our prediction that Leopard Cat movement would be negatively influenced by rodent biomass. This finding, however, may be an artefact of our data collection. Although we did not target dirt roads, there was an abundance of dirt roads within the reforested area due to its artificial nature, and one camera in the reforested area was placed (at random) near a dirt road (<10m). This camera alone recorded 50% of our reforested area individuals and 100% of the reforested area's recaptures. Thus, the finding that the Leopard Cat movement was lower in the reforested area likely stems from the absence of recaptures at different camera sites. Based on this experience, we recommend that future studies targeting Leopard Cats implement stratified study designs whereby camera traps are placed both on and off roads to explicitly explore differences in Leopard Cat density, capture probability, and movement.

Consistent with our predictions, our second topranked model [D(*habitat*) g0(b) $\sigma(.)$] does indicate that Leopard Cat density varied by habitat type in a manner that reflects prey availability, with both average rodent biomass and Leopard Cat density being 2.7 times higher in the evergreen compared with the reforested areas. Only two detections (out of 4,063 trap nights), however, came from Sakaerat's dry dipterocarp forest, the habitat with the second highest estimate of rodent biomass. Rabinowitz (1990) similarly observed Leopard Cats using dry dipterocarp forest less than other habitat types, noting that the dipterocarp contained lower densities of the Red Spiny Rat *Maxomys surifer*, the main prey item of Leopard Cats during that study. Results from rodent trapping in the current study had similar findings, with *M. surifer* being the most frequently captured rodent in both evergreen (100% of captures) and reforested areas (89.1% of captures), but only a few captures in the dipterocarp (3% of captures).

In addition to having the lowest capture rate of a key Leopard Cat prey species, the dipterocarp also had relatively high encounter rates for three sympatric small carnivore species: Golden Jackal *Canis aureus*, Javan Mongoose *Herpestes javanicus*, and Small Indian Civet *Viverricula indica* (Appendix A). Although direct evidence of competition between these three species and Leopard Cats was not reported, interspecific competition among other sympatric carnivores is welldocumented within the literature (Palomares & Caro 1998; Donadio & Buskirk 2006). Future studies should be careful to account for both the prey community and the potential for interspecific competition among sympatric small carnivores when considering the suitability of a specific patch of forest for Leopard Cats.

Leopard Cats and degraded forests

With an estimate of 17.7 individuals/100km² overall and 21.2 individuals/100km² in the evergreen, Sakaerat supports the highest recorded SECR-derived Leopard Cat density to date (range from other studies: 2.9–17.0 individuals/100km²; Table 3). These findings corroborate other studies which also found Leopard Cat densities to be higher in more degraded environments (Mohamed et al. 2013; Srivathsa et al. 2015). Srivathsa et al. (2015), for example, compared Leopard Cat densities in four protected areas in India, finding higher densities clustered around secondary, disturbed, or partially modified forests. Bhadra Tiger Reserve, which supported the study's highest Leopard Cat density (10.5 individuals/100km²), consists predominantly of semi-evergreen forest still recovering from the voluntary resettlement of 26 forest villages in 2002 and currently adjoins large tracts of coffee plantations and several unprotected forest reserves (Srivathsa et al. 2015). Similarly, Mohamed et al. (2013) recorded a higher Leopard Cat density in more intensively logged commercial forest reserves (12.4 individuals/100km² and 16.5 individuals/100km²) compared to a more sustainably logged reserve (9.6 individuals/100km²) in Sabah, Malaysian Borneo.

It is hypothesized that the Leopard Cat's association with degraded environments is related to elevated rodent populations within such areas (Lambert et al. 2006; Rajaratnam et al. 2007; Wells et al. 2007; Pimsai et al. 2014), given the tendency for murid rodents to be key prey items of Leopard Cats (Rabinowitz 1990; Grassman et al. 2005; Rajaratnam et al. 2007; Shehzad et al. 2012). Researchers and conservationists, however, should be careful when interpreting these general findings as not all degraded areas are alike. Oil palm plantations, for example, support abnormally high murid rodent densities, which in some cases can exceed 100 individuals/ha, whereas during our study the highest recorded density within the evergreen was only 10.5 individuals/ha (Wood & Fee 2003; Scott et al. 2004). Variation in prey communities among degraded habitats may also play a deciding role in habitat selection among Leopard Cats. As mentioned previously, Leopard Cat encounter rates in our study strongly reflected capture rates of *M. surifer*, which were highest in the evergreen and lowest in the dipterocarp. This emphasis on a specific murid species as primary prey was documented previously for Leopard Cats in Thailand (Rabinowitz 1990), Japan (Yasuma 1981), and Malaysian Borneo (Rajaratnam et al. 2007). Similar findings were also documented in other tropical small felids, including

Serval *Leptailurus serval* (Geertsema 1985), Jaguarundi *Herpailurus yagouaroundi* (Konecny 1989), and Guigna *Leopardus guigna* (Dunstone et al. 2002).

Other proposed factors influencing whether the habitat is suitable for Leopard Cats include habitat structure and its effect on prey 'catchability' (Rajaratnam et al. 2007). In addition to supporting high murid densities, oil palm plantations are notable for being relatively free of understory vegetation, potentially facilitating successful predation events (Rajaratnam et al. 2007). This may be relevant to our study's findings due to the ubiquity of tall dense bamboo Arundinaria pusilla within Sakaerat's dipterocarp forest. If the presence of this grass reduced the catchability of prey in the dipterocarp, it may potentially explain why so few Leopard Cats were recorded in this habitat. Although we lack evidence to directly support this hypothesis, studies of other felids demonstrated a preference for habitats with high prey catchability over areas with high prey availability (e.g., Cheetah Acinonyx jubatus, Broomhall et al. 2003; Lion Panthera leo, Hopcraft et al. 2005).

Leopard Cats tolerate habitat degradation and even associate with specific human land uses such as oil palm (Ross et al. 2010) and sugar cane plantations (Lorica & Heaney 2013) and logged forests (Ross et al. 2010; Mohamed et al. 2013). Yet, despite a growing body of literature, their habitat requirements, population sizes, and long-term viability within both degraded forests and agriculture habitats remain unclear. Our study not only contributes to the current need for information on population density and habitat selection within forest fragments but also supports the idea that forest fragments may be crucial for the conservation of Leopard Cats in human-dominated landscapes. More research, however, is needed concerning the long-term viability of these populations. To fill this crucial knowledge gap, we recommend future studies leave the confines of protected areas in order to investigate the role their surroundings play both as habitat and as facilitators of connectivity.

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Appendix A. Encounter rates (independent detections/100 trap nights) of four species of small carnivores, by forest type and period of resource availability, in Sakaerat Biosphere Reserve, Thailand, 2017. Images were classified as "independent detections" only if the time between images was greater than or equal to 30min (O'Brien et al. 2003).

	Dipterocarp	Evergreen	Reforested
Leopard Cat	0.1	0.7	0.6
Golden Jackal	2.5	0.8	15.9
Javan Mongoose	19.6	0.0	0.2
Small Indian Civet	3.2	0.2	0.4

Appendix B. Full model selection for Leopard Cat 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	к	AIC _c	ΔAIC _c	w,
D(.) g0(b) sigma(habitat)	5	961.17	0.00	0.43
D(habitat) g0(b) sigma(.)	5	962.69	1.52	0.20
D(.) g0(.) sigma(<i>habitat</i>)	4	963.66	2.49	0.12
D(.) g0(habitat) sigma(habitat)	5	964.69	3.52	0.07
D(habitat) g0(.) sigma(habitat)	5	965.94	4.77	0.04
D(habitat) g0(.) sigma(.)	4	966.12	4.94	0.04
D(.) g0(<i>habitat</i> + <i>bk</i>) sigma(.)	5	966.30	5.13	0.03
D(.) g0(<i>habitat</i> + <i>b</i>) sigma(.)	5	966.76	5.59	0.03
D(.) g0(habitat) sigma(.)	4	967.88	6.70	0.02
D(habitat) g0(habitat) sigma(.)	5	968.61	7.44	0.01
D(.) g0(<i>b</i>) sigma(.)	4	970.67	9.50	0.00
D(.) g0(b) sigma(season)	5	971.29	10.12	0.00
D(.) g0(bk) sigma(.)	4	972.55	11.38	0.00
D(.) g0(b) sigma(rodent biomass)	5	973.98	12.80	0.00
D(.) g0(.) sigma(.)	3	974.20	13.03	0.00
D(.) g0(.) sigma(season)	4	975.05	13.88	0.00
D(season) g0(.) sigma(.)	4	975.83	14.66	0.00
D(.) g0(season) sigma(season)	4	976.18	15.01	0.00
D(.) g0(B) sigma(.)	4	976.26	15.09	0.00
D(.) gO(.) sigma(rodent biomass)	4	976.31	15.14	0.00
D(.) g0(rodent biomass) sigma(.)	4	976.42	15.25	0.00
D(.) g0(<i>Bk</i>) sigma(.)	4	976.49	15.32	0.00







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