Received: 8 July 2022 | Revised: 10 August 2022 | Accepted: 24 August 2022

DOI: 10.1002/ecs2.4338

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Ecosphere Naturalist

Marbled cats in Southeast Asia: Are diurnal and semi-arboreal felids at greater risk from human disturbances?

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Funding information
Australian Research Council, Grant/Award Number: DECRA #DE210101440; Nanyang Technological University; National Geographic Society Committee for Research and Exploration, Grant/Award Number: 9384-13; Smithsonian Institution; The University of Queensland

Handling Editor: Elizabeth Flaherty

Abstract

Southeast Asia supports the greatest diversity of felids globally, but this diversity is threatened by the severe forest loss and degradation occurring in the region. The response of felids to disturbances appears to differ depending on their ecology. For example, the largely terrestrial and nocturnal leopard cat (*Prionailurus bengalensis*) thrives near forest edges and in oil palm plantations where it hunts rodents (Muridae) at night, thereby avoiding human activity peaks. Conversely, we hypothesized that the sympatric and similar-sized marbled cat (*Pardofelis marmorata*) would respond negatively to edges and relatively open oil palm plantations as they are more arboreal than leopard cats, rely on tree connectivity for hunting, and are diurnal so have less potential to temporally avoid humans. We used camera trapping from Southeast Asia to test habitat associations at multiple spatial scales using zero-inflated Poisson generalized linear mixed models and hierarchical occupancy modeling. We found that marbled cats were positively associated with large intact forests and, in contrast to leopard cats, negatively associated with oil palm plantations. Furthermore, we found preliminary evidence suggesting marbled cats may adapt their diel activity to become more crepuscular in degraded forests, likely shifting their activity to avoid humans. These findings suggest that the marbled cat's International Union for Conservation of Nature (IUCN) Red List conservation status should potentially be upgraded from Near Threatened to Vulnerable, matching other forest-dependent felids in the region. We posit our findings may be generalizable such that semi-arboreal and diurnal felids could face greater threats from habitat degradation than their terrestrial and nocturnal relatives.

KEYWORDS
camera trapping, diel activity patterns, habitat associations, occupancy modeling, small cat conservation, tropical East Asia

INTRODUCTION

Humans are altering wildlife habitats and behaviors globally (Gaynor et al., 2018; Grantham et al., 2020; Plumptre et al., 2021). This threatens many species, but others are tolerant to, or may even benefit from, habitat disturbances and human activities (Hunter, 2007; Peh et al., 2006; Suraci et al., 2019). Elucidating the traits that make species vulnerable to anthropogenic disturbance will be critical for identifying conservation priorities in the coming decades (Beissinger, 2000; Keinath et al., 2017).

There are numerous examples of related species exhibiting disparate responses to disturbances and human activity, thus providing opportunities for comparative analyses that can improve our understanding of the traits that mediate responses to anthropogenic disturbances (Frey et al., 2020; Heim et al., 2019). For example, some tropical felids, such as the leopard cat (*Prionailurus bengalensis*) in Southeast Asia and the ocelot (*Leopardus pardalis*) and jaguarundi (*Herpailurus yagouaroundi*) in the neotropics, are tolerant of fragmented and degraded landscapes and have been detected within oil palm plantations and nearby forests (Jennings et al., 2015; Mendes-Oliveira et al., 2017; Pardo et al., 2021; Silmi et al., 2021). Conversely, other tropical felids are detected far less frequently or not at all in oil palm plantations and other disturbed landscapes, such as the tiger (*Panthera tigris*), clouded leopard (*Neofelis* sp.), and Asiatic golden cat (*Catopuma temminckii*) in Southeast Asia and the margay (*Leopardus wiedii*) in the neotropics (Jennings et al., 2015; Luskin et al., 2017; McCarthy et al., 2015; Mendes-Oliveira et al., 2017; Yue et al., 2015). It is not clear why some tropical felids can adapt to disturbed landscapes while others cannot, although there appears to be a pattern wherein the more adaptable tropical felids are often terrestrial and nocturnal, while the intolerant species are usually semi-arboreal and diurnal (Table 1).

One such semi-arboreal and diurnal tropical felid is the marbled cat (*Pardofelis marmorata*) (Figure 1). The marbled cat inhabits an extensive range across Asia that extends eastward from the foothills of the Himalayas and south to Borneo. The species occurs in a variety of forest types including tropical montane forest (Pusparini et al., 2014), peat swamp forest (Cheyne & Macdonald, 2011; Jeffers et al., 2019), bamboo forest (McCann, 2016), recently logged forests (Hearn et al., 2016; Mohamed et al., 2009; Wearn et al., 2013), and at elevations up to 2000 m (Haidir et al., 2021; Hearn et al., 2018; Johnson et al., 2009; Pusparini et al., 2014; Sunarto et al., 2015). The marbled cat is currently listed as Near Threatened on the International Union for Conservation of Nature (IUCN) Red List (RL) because its population is thought to be declining due to habitat loss (Castelló et al., 2020; Ross et al., 2016). This benign threat status is surprising because most sympatric felids are listed as Vulnerable or Endangered (Table 1), except for the leopard cat (Least Concern) which is known to occur in degraded habitats (Jennings et al., 2015; Silmi et al., 2021). The marbled cat is generally agreed to be forest dependent, and some research has suggested the species avoids edges and humans (Hearn et al., 2016; Ross et al., 2016). It is also possible that the marbled cat's arboreal diurnal prey (e.g., squirrels, tree shrews, and birds) may not thrive in plantations to the degree of some terrestrial nocturnal prey like Muridae species (Fitzherbert et al., 2008). Taken together, it remains unclear whether observations of marbled cats in logged forests demonstrate that the species is at least somewhat tolerant of habitat degradation (similar to sympatric leopard cats) or if these observations represent aberrations from more general trends showing avoidance of disturbed areas.

While the behavior and diet of the marbled cat are poorly understood, its morphology, notably a long tail to provide balance while climbing trees and the ability to rotate its paws 180° to descend from trees headfirst, is indicative of an arboreal nature (Hearn et al., 2018; Kitchener et al., 2010; Mohamed et al., 2009). The marbled cat is believed to be diurnal (Lynam et al., 2013; Singh & Macdonald, 2017; Sunarto et al., 2015) and primarily prey on other diurnal and arboreal species such as lizards, birds, tree shrews, and squirrels (Castelló et al., 2020; Mukherjee et al., 2019; Rasphone et al., 2020; Ross et al., 2016). Small, terrestrial mammals also appear to be part of the marbled cat's diet (Davis, 1962). Observational and co-occurrence data suggest that marbled cats may also prey on larger bodied arboreal species such as primates (Borries et al., 2014; Hearn et al., 2018).

Here we investigate if differing felid ecologies can explain differing responses to disturbances. We posit that semi-arboreal felids, such as the marbled cat, may be more sensitive to deforestation and habitat degradation

TABLE 1 The ecology and International Union for Conservation of Nature (IUCN) Red List conservation status of Southeast Asian felids, adapted from Castelló et al. (2020).

Felid	Mass (kg)	Ecology	Southeast Asian range	IUCN Red List status
Tiger *Panthera tigris*	75–140	Terrestrial, nocturnal	Mainland, Sumatra	Endangered
Common leopard *Panthera pardus*	25–55	Semi-arboreal, nocturnal	Mainland, Java	Vulnerable
Mainland clouded leopard *Neofelis nebulosa*	11.5–18	Semi-arboreal, nocturnal	Mainland	Vulnerable
Sunda clouded leopard *Neofelis diardi*	12–23	Semi-arboreal, nocturnal	Sumatra, Borneo	Vulnerable
Asiatic golden cat *Catopuma temminckii*	8.1–15.7	Terrestrial, diurnal/crepuscular	Mainland, Sumatra	Near Threatened
Bay cat *Catopuma badia*	3–5	Terrestrial, diurnal	Borneo	Endangered
Marbled cat *Pardofelis marmorata*	2–5	Semi-arboreal, diurnal	Mainland, Sumatra, Borneo	Near Threatened
Fishing cat *Prionailurus viverrinus*	5.1–16	Terrestrial, nocturnal	Mainland, Java	Vulnerable
Flat-headed cat *Prionailurus planiceps*	1.5–2.7	Terrestrial, nocturnal/crepuscular	Mainland, Sumatra, Borneo	Endangered
Leopard cat *Prionailurus bengalensis*	0.5–3.8	Terrestrial, nocturnal/crepuscular	Mainland, Borneo, Sumatra, Java	Least Concern

FIGURE 1 Camera trap images of marbled cats from our new surveys in Bukit Barisan Selatan National Park in southern Sumatra in 2014 (cropped to better show the species morphology): (a) a typical "blotched" marbled cat coat pattern and (b) the rarer melanistic morph. Photo credit: M. Luskin, 2014.

as they rely upon tree connectivity for hunting (Whitworth et al., 2019), whereas diurnal felids may be more negatively impacted by humans that are mostly active during the day (Suraci et al., 2019; Wang et al., 2015). To provide insight into these hypotheses, we examined the habitat associations and diel behavior of the marbled cat, and compare this to a related species, the leopard cat, which is a sympatric, similar-sized, and more well-studied felid.

To examine the habitat associations and behavior of marbled cats, we gathered occurrence records from a thorough review of published records as well as from 21 new camera trapping surveys conducted in the marbled cat's range. Given most forested areas in the region are now degraded to some extent by fragmentation and/or proximity to oil palm plantations (Grantham et al., 2020; Haddad et al., 2015; Miettinen et al., 2012; Wilcove et al., 2013), understanding the marbled cat's regional- and local-scale habitat associations and the effects of habitat degradation is crucial for accurately determining the species conservation status and, in turn, conserving this species. Therefore, we tested whether marbled cat regional detections and local occupancy were negatively affected by forest degradation and oil palm plantations, as well as other environmental covariates. We also compared the marbled cat's diel activity at degraded and nondegraded sites, hypothesizing they would exhibit a shift away from diurnal activity in degraded habitats to avoid encounters with humans who are more likely to be present during the day in degraded forests, as shown for many other species (Gaynor et al., 2018). To answer our questions on regional habitat associations, we conducted species distribution modeling (SDM) using Maxent, and then also assessed if variations in camera trap detections were explained by abiotic and anthropogenic variables. We assessed the influence of local variables using detection-corrected hierarchal occupancy modeling based on the camera-level detection histories from the new camera trapping surveys where the marbled cat was detected. We also used these new camera trapping data to assess the diel activity of the marbled cat and its prey.

MATERIALS AND METHODS

Methods were replicated from Dehaudt et al. (2022) and Dunn et al. (2022).

Data collection

We defined our Southeast Asian study region as including Myanmar, Thailand, Cambodia, Laos, Peninsular Malaysia, Singapore, Sumatra, and Borneo. We compiled presence data on the marbled cat from four sources: (1) detections recorded in previously published camera trapping studies; (2) detections from new camera trapping sessions conducted across seven landscapes in Southeast Asia; (3) presence-only data from the Global Biodiversity Information Facility database (GBIF, 2019) such as museum records and verified scientific observations; (4) presence-only data from the Borneo Carnivore Database (Rustam et al., 2016). Presence data were the coordinates of a location where the marbled cat was observed any number of times within the course of a camera trapping study or otherwise reported to be present. A camera trapping study was defined as continuous sampling within a landscape (10–1000 km^2) using at least five cameras. The term "landscape" refers to an area where sampling occurred such as a national park, a production forest, or a collection of forest patches in and around oil palm or other agricultural plantations.

Collating published camera trapping studies for regional analyses

We compiled published camera trap records by searching Web of Science with the following criteria: "camera trap* AND Asia* or Thai* or Malaysia* or Indonesia* or Singapore* or Borneo* or Cambodia* or Vietnam* or Lao* or Myanmar* or Burm* or Sumatra* or Borneo*." We selected from the list of returned studies those that were written in English and reported relevant results for the marbled cat, including sampling effort (number of cameras, and deployment length or total trap nights) and number of independent detections (generally defined based on a 30–60 min interval between detections of the same species, referred to as "independence period"). We examined the references listed in key papers to identify and include further sources. We included all tropical forest camera trapping studies that used unbaited cameras placed <0.4 m height, usually facing trails or other areas determined by researchers to be used by wildlife. This is the standard deployment approach widely used in the region and is suitable for the majority of semiterrestrial species >1 kg (Rovero & Ahumada, 2017). From each study, we recorded the location (landscape name and coordinates), detection and effort data, and a variety of other covariates available. We grouped multiple studies from the same landscape per year by summing detections and effort among the studies and averaging the covariate values.

New camera trapping sessions

We conducted 21 new camera trapping sessions in 10 tropical forest landscapes in Thailand, Peninsular Malaysia, Sumatra, Borneo, and Singapore between December 2013 and June 2020. Of these 18 sessions in seven different landscapes occurred in the marbled cat's IUCN range. Camera trapping in three locations outside the marbled cat's IUCN range allowed us to investigate whether the marbled cat has recolonized any regions that it may have been extirpated from. We deployed between 18 and 78 passive infrared Bushnell Trophy and Reconyx HC500 Hyperfire camera traps cross sampling areas ranging from 10 to 813 km^2. We standardized deployment methods across all landscapes (see Appendix S1: Table S1 for summary data on landscape characteristics). Camera traps were spaced at least 500 m apart in large landscapes (>50 km^2) and 100–500 m apart in smaller landscapes to maximize spatial coverage. Camera traps were attached to trees 0.3 m above the ground along trails (both wildlife and hiking trails) and deployed for approximately 60–90 days. We considered detections independent if they occurred at least 30 min apart. Permit numbers are provided in Appendix S1: Table S2. Our universities did not require ethical approval for noninvasive camera trapping.

Mapping, range, and probability of presence

First, to provide an update to the marbled cat's "extent of occurrence" (EOO), we extracted the range shapefile from the IUCN website (dated 2015) and calculated the area of remaining tree cover in our Southeast Asian study area as of in 2015. We also calculated the percentage of protected forest within the marbled cat's Southeast Asian range, based on the IUCN World Database on Protected Areas (UNEP-WCMC and IUCN, 2021). Then, we used SDMs to map the probability of presence for the marbled cat using Maxent (version 3.4.4) (Phillips et al., 2006), using presence data only and 10 GIS spatial layers (Appendix S1: Table S3). We removed records from before the year 2000 to avoid including areas where the marbled cat may no longer be present due to recent deforestation. The GIS layers we used included both biogeographical factors such as elevation, landscape cover, mean annual rainfall, and forest cover and anthropogenic factors such as human population density and oil palm cover (Appendix S1: Table S3). Model performance was tested using receiver operating characteristic (ROC) analysis, with 15% of the data set aside. We reported the relative contribution of each predictor to the probability of presence model using Jackknife training gain test results and followed Maxent guidelines in reporting the log–log output for mapping, clipping the output to show probability of presence only in remaining forest using QGIS.

Assessing regional habitat associations with generalized linear mixed models

We used both the published and new camera trap data to investigate regional-scale relationships between the number of marbled cat detections and various environmental and anthropogenic factors using generalized linear mixed models (GLMMs) with zero-inflated Poisson error distribution. We treated detections as count data and used a Poisson error distribution and included fixed continuous term to control for study effort (measured in trap nights) and a random categorical term for landscape, because some landscapes had multiple observations. Following Ash et al. (2020), our response variable was the raw count data as opposed to a relative abundance index (RAI, usually independent detections per 100 trap nights). We note that such methods do not account for differences in detection probability between studies and thus do not reflect true abundance of wildlife (Sollmann et al., 2013). For this analysis, we are therefore implicitly assuming that detection probability among camera traps and studies is constant and acknowledge this may result in some inaccuracy. We also acknowledge that variation in detections can arise due to differences in equipment and deployment methodology between studies. Both of these sources of measurement error may reduce our modeling power and our chances of detecting "true" relationships.

We used GLMMs to test the effect of 10 environment and anthropogenic descriptor variables on marbled cat detections among landscapes. Our covariate values were derived from GIS layers and describe the area within a 20-km radius around the centroid of each landscape (Appendix S1: Table S2). We used this vast study area ($1256\ km^2$) to account for the low resolution of centroid coordinates provided or inferred by some studies. Our spatial covariates included previously described layers from Maxent analysis, plus forest size (in square kilometers; Appendix S1: Table S3). We tested each variable with linear and nonlinear models and used corrected Akaike information criterion (AIC_c) model selection to identify the most parsimonious models (Burnham & Anderson, 2002). We addressed collinearity by not running multivariate models. All GLMMs were implemented in the R package "GLMMadaptive" in R (version 4.0.4) (R Core Team, 2020; Rizopoulos, 2019).

Assessing local-scale habitat associations using occupancy modeling

We produced a detection history matrix for the marbled cat based on a sampling occasion of five days and containing presence/absence data (0 = marbled cat not detected; 1 = marbled cat detected; NA = inactive sampling unit or occasion). We assessed the effect of habitat variables on marbled cat occupancy at the local scale within landscapes, using single-season, single-species occupancy modeling (MacKenzie et al., 2002). As with our GLMM modeling, we addressed collinearity by not running multivariate models. We overcome the low detection probability expected when studying mostly arboreal marbled cats using ground-based cameras with our immense trapping effort. Furthermore ground-based camera traps have been previously shown to record the majority of arboreal mammals at the area of deployment (Moore et al., 2020), including primates and squirrels, which are thought to be marbled cat prey. To satisfy the requirement of spatial independence of our camera traps, we resampled all new camera trapping data into 3.45 km^2 hexagonal grid cells with an apothem of 1 km, defined as our sampling units. In most cases, each sampling unit (hexagon) contained only one camera, but for those with two or more, wildlife detection histories were grouped together according to which sampling unit they occurred in, and we averaged their covariate values. We included study as a fixed effect to maintain the spatial and temporal independence of our sampling units and satisfy the assumption of population closure in the models. In addition to the variables described previously, we tested the effect of local-scale predictors such as distance to forest edge and distance to river and used AIC_c to identify the most parsimonious model (implemented in the R packaged "unmarked") (Fiske & Chandler, 2011). All covariates were standardized.

Analysis of diel activity patterns

We used time-stamped detections from our new camera trapping to investigate the marbled cat's diel activity and to compare this to potential prey. Prey animals were grouped into the categories of "bird," "terrestrial mammal," and "arboreal mammal." Pig-tailed macaques (*Macaca nemestrina*) were assessed separately as juvenile pig-tailed macaques have previously been identified as a likely marbled cat prey item (Hearn et al., 2018). We computed von Mises kernel density estimates in R using the densityPlot() function from the "overlap" package (Meredith & Ridout, 2020) with default smoothing parameters. To compare how activity patterns of marbled cats overlap with potential prey species, we computed coefficients of overlapping following Ridout and Linkie (2009). We also tested whether degradation affects the marbled cat's diel activity by comparing the activity of marbled cats in degraded and nondegraded (intact) forests. Specifically, we divided marbled cat detections into two categories (degraded and nondegraded) depending on whether the value of the forest degradation variable associated with a marbled cat detection was above or below the median value of the forest degradation variable for all marbled cat detections. Forest degradation was defined as the percent combined cover of oil palm plantations, lowland mosaic forest, lowland open ground, and regrowth forests within a 1.0-km radius of a camera trap in our new camera trapping sessions. We ran a bootstrap procedure to simulate 1000 marbled cat activity pattern distributions, then conducted a Wald test using the compareAct() function in the R package "activity" (Rowcliffe et al., 2014). The coefficient of overlap was calculated using the R package "overlap" (Ridout & Linkie, 2009).

RESULTS

Detections of marbled cats

We gathered a total of 161 geo-referenced occurrence records for the marbled cat, consisting of 59 from previously published camera trapping studies, 45 from new camera trapping, 50 from the Borneo Carnivore Database, and 7 from GBIF (Table 2). In our new camera trapping sessions, the marbled cat was detected at seven different landscapes, all of which are part of its IUCN range. All detections were of solitary individuals except for one detection of a pair, likely a mother and cub, at Bukit Barisan Selatan National Park in southern Sumatra. In our new sessions, the marbled cat was most common in Bukit Barisan Selatan National Park (13 detections and 0.226 independent detections per 100 trap nights, hereafter just "RAI"; naïve occupancies per landscape and survey are provided in Appendix S1: Table S4).

EOO, area of occupancy, and probability of presence

We measured the marbled cat's IUCN RL EOO in the study region to be 1,143,940 km^2 (Table 3). The forested area remaining inside the IUCN RL EOO was 742,926 km^2 (updated EOO), which is 35.1% smaller compared with the IUCN range published in 2015 (Figure 2d).

TABLE 2 Data sources and sample sizes for the analyses done in this study.

Analysis	Detections
Presence data for Maxent modeling (no. records)	126
Global Biodiversity Information Facility	7
Borneo Carnivore Database	50
Published camera trap study presences	59
New camera trap study presences	10
Count data for GLMMs[a] (no. camera studies within its range)	67
Independent detections used for occupancy modeling	42
No. landscapes with sufficient detections for occupancy models	7
No. trapping sessions with sufficient detections for occupancy modeling	12
Independent detections for activity patterns[b]	45

Abbreviation: GLMMs, generalized linear mixed models.

[a]Detection data from the new camera trapping datasets were included in the GLMM analysis.

[b]Activity pattern analyses were performed using only new camera trapping data.

TABLE 3 Area of marbled cat range and forest cover in different regions of Southeast Asia.

Region	Extent of occurrence: IUCN RL in 2015 (km^2)	Extent of occurrence: Updated (km^2)	Percentage forested	Percentage protected forest
Borneo	336,928	259,675	77.1	12.3
Continental Southeast Asia	602,501	375,539	62.3	21
Peninsular Malaysia	60,904	37,876	62.2	23.6
Sumatra	143,607	69,836	48.6	20.3
Southeast Asia total	1,143,940	742,926	64.9	18.5

Note: The International Union for Conservation of Nature Red List (IUCN RL) extent of occurrence (EOO) is the species range in each region. Updated EOO is the area of occupancy, defined here as the forested area remaining within the IUCN RL EOO in 2015 (Miettinen et al., 2016), which is an overestimate because it assumes all remaining forest is occupied. Therefore, it may be interpreted more correctly as the remaining habitat available. "Percentage forested" is the EOO divided by the IUCN RL EOO and the "Percentage protected forest" is the forested area within protected areas divided by the IUCN RL EOO.

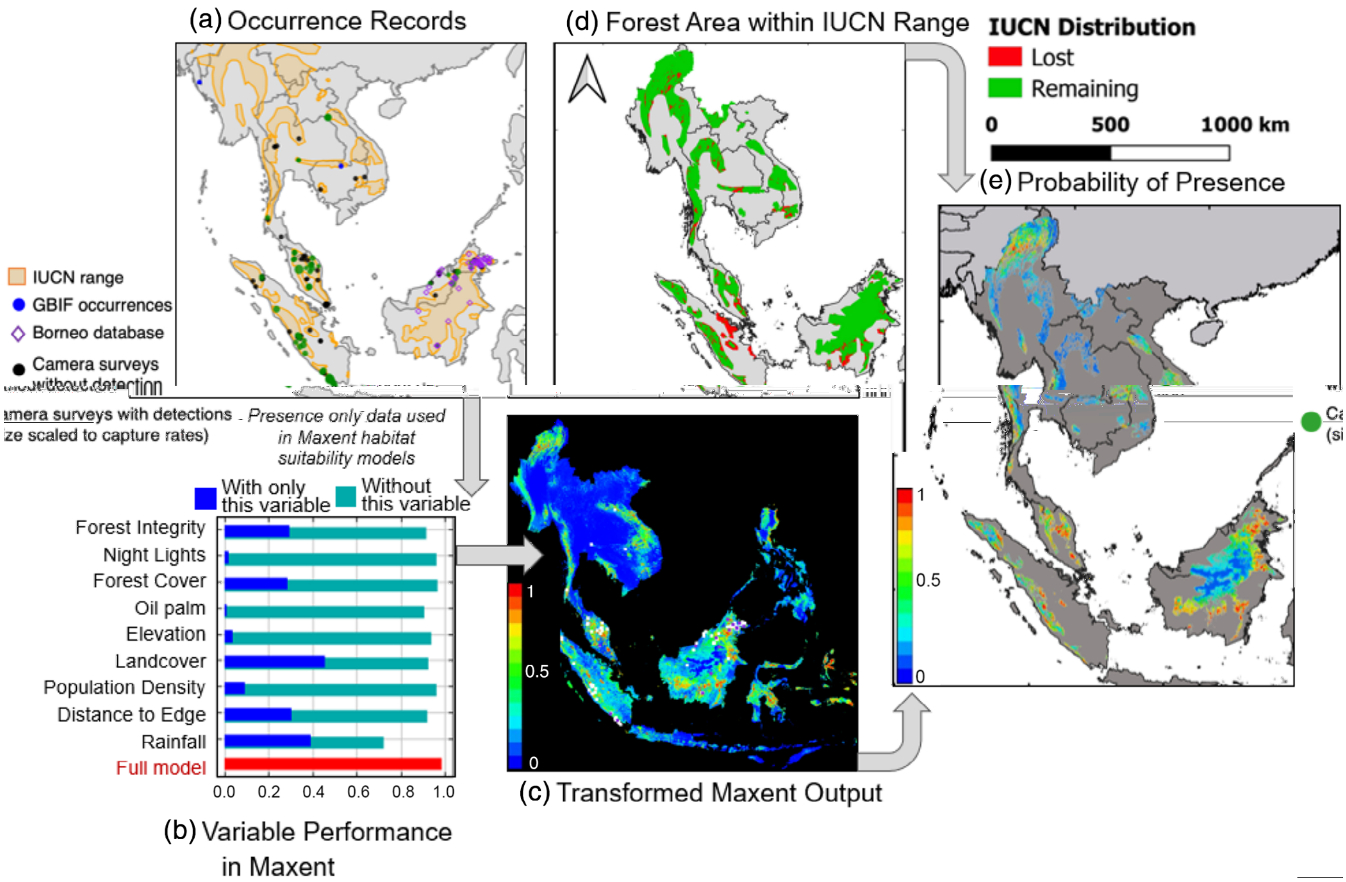

FIGURE 2 Marbled cat probability of presence within remaining forest in Southeast Asia. (a) The International Union for Conservation of Nature (IUCN) Red List range of the marbled cat from 2015 is shaded in orange. This area is the species extent of occurrence or "EOO." The location of marbled cat occurrence records, colored by source (see key) is also shown (Borneo database: Rustam et al., 2016). (b) The performance of all variables tested in the Maxent probability of presence modeling in the form of a jackknife graph using the regularized training gain. The dark blue bars show the training grain of a model including only the variable in question, whereas the teal bars show the predictive power of the full model excluding the denoted variable. These teal bars highlight whether this variable captures unique information. (c) The output of Maxent modeling, specifically the predicted probability of presence of the marbled cat in Southeast Asia, including deforested and other nonforested areas. (d) The areas of the marbled cat's range in Southeast Asia that were forested in 2015 (green) and those that are no longer forested (red). (e) The probability of presence of the marbled cat within remaining forest with nonforested areas assumed to be unoccupied by this species. GBIF, Global Biodiversity Information Facility.

Only 18.5% of the marbled cat's IUCN RL range in our Southeast Asian study region is protected forest.

The marbled cat's predicted probability of presence within remaining forests across the study region was uneven, with notable pockets of high probability of presence (>0.8) in Borneo (southern Kalimantan and Sabah), Peninsular Malaysia, and northern Myanmar. Areas with low probability of presence (<0.1) included central Myanmar, northern Thailand, and central Borneo. The variables containing the highest amount of information when modeled in isolation were landscape cover, followed by annual precipitation, distance to edge, Forest Landscape Integrity Index (FLII), and forest cover (Figure 2b). Forest cover and FLII positively influenced the probability of presence, and the influence of rainfall was greatest at median values (2200–3000 mm of annual rainfall) rather than extremes resulting in a bell-shaped response curve. Notably, only omitting rainfall markedly decreased model performance, suggesting that this variable contributes to a unique explanatory power (Figure 2b). The Maxent model performance was very high (area under the curve [AUC] for the ROC curve on the test data = 0.819; Appendix S1: Figure S1).

Regional occurrence predictors

We used GLMMs with capture data from 85 camera trapping surveys (289,978 trap nights) to assess the relationship between marbled cat detections and landscape descriptors. Oil palm was the best predictor of marbled cat detections with a significant and negative relationship ($\beta = -0.64 \pm 0.17$, $p < 0.001$; Table 4; Figure 3a) based on AIC_c. The next best models were forest size ($\beta = +0.45 \pm 0.15$, $p = 0.002$) and forest cover ($\beta = +0.71 \pm 0.24$, $p = 0.004$), which both had a positive effect on marbled cat detections.

Variation in local-scale occupancy

For our new camera trapping, the highest occupancy was observed in Danum Valley (0.154) and the lowest—among those sites with at least one detection—were Ulu Muda (specifically the 2016a study) and Pasoh Forest Reserve (both 0.017; Appendix S1: Table S4). We did not identify any variable with a significant ($p < 0.05$) effect on marbled cat local occupancy, but elevation was the best predictor based on AIC_c model selection (Table 5) and showed a positive relationship ($\beta = 1.728 \pm 1.19$, $p = 0.145$) (Figure 3d).

TABLE 4 Variables associated with regional camera trap detections of marbled cats in Southeast Asia.

Model	K	LLk	AIC_c	ΔAIC_c	AIC_c weight
Oil palm	4	−127.8	267.80	0.0	0.72
Forest size (log)	4	−131.10	274.20	6.40	0.03
Forest cover	4	−131.20	274.40	6.60	0.03
Elevation	4	−132.50	277.10	9.30	0.01
Forest integrity^2	4	−131.60	278.21	10.41	0.00
Forest intactness^2	4	−132.54	280.08	12.28	0.00
Nighttime lights	4	−134.40	280.90	13.10	0.00
Landscape roughness^2	4	−134.42	283.83	16.03	0.00
Null	3	−137.30	284.00	16.20	0.00

Note: Univariate model selection criteria (AIC_c) from the zero-inflated Poisson generalized linear mixed model assessing variation in independent detections of the marbled cat, including study effort and landscape as random effects. All covariates were averaged for the area in a 20-km radius around the centroid of the study landscape for each survey, then standardized so effect sizes can be meaningfully compared. Independent detections are usually defined as photos separated by 20–60 min. All models included the same data (67 observations from 34 landscapes). We tested linear and nonlinear responses for all covariates and only include the better-performing model. Nonlinear models are denoted by a superscript 2. Abbreviations: AIC_c, corrected Akaike information criterion; LLk, log likelihood.

Diel activity patterns of the marbled cat

Marbled cats were strongly diurnal and had very high ($\Delta_1 > 0.8$) overlap with birds and arboreal mammals (highest for pig-tailed macaques) and low overlap with small terrestrial mammals ($0.4 > \Delta_1 > 0.2$) (Figure 4). Their peak activity in intact forests was just after midday, but this shifted to a peak activity a few hours after sunrise in degraded forests although this large shift was not statistically significant (Figure 5).

DISCUSSION

This study leveraged the largest dataset on marbled cats yet compiled to uncover compelling evidence that the species is forest dependent and negatively impacted by habitat degradation and oil palm plantations. This is not surprising because logged forests and oil palm plantations lack the tree connectivity and canopy complexity of intact forests that semi-arboreal marbled cats may prefer (Korol et al., 2021; Luskin & Potts, 2011). Marbled cats also appear to shift their activity patterns in degraded forests (Figure 5), likely to avoid interactions with humans; however, the shift was not statistically significant because

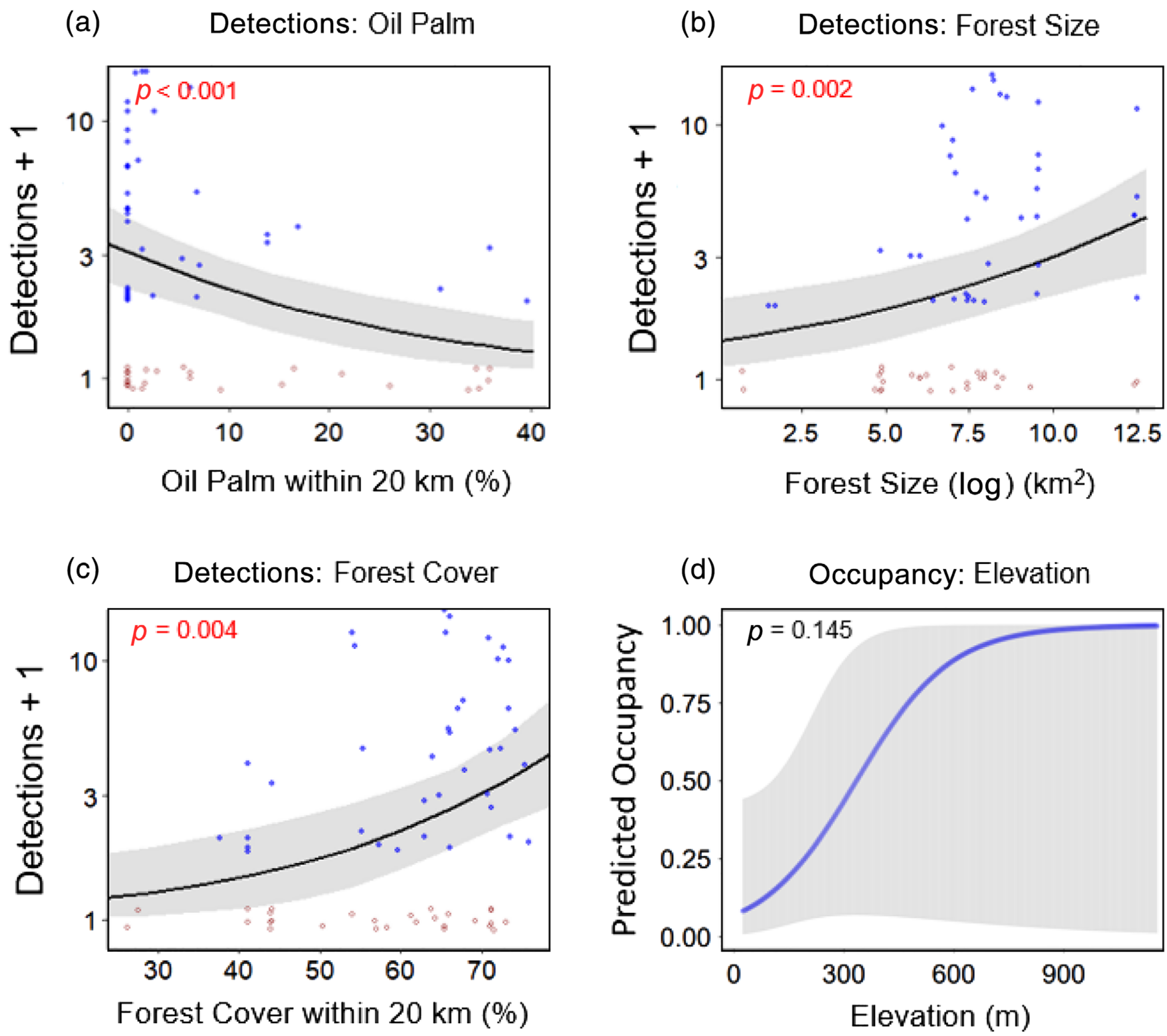

FIGURE 3 Predictors of marbled cat regional detections (a–c) and local occupancy (d). All covariates were centered and standardized prior to modeling, so effect sizes can be compared. *p* values are reported based on the *z* values of the covariates. *p* values colored red are significant whereas those colored black are not significant. Regional responses come from the zero-inflated Poisson generalized linear mixed models assessing variation in detections for entire studies. Trend lines were drawn using the predict() function in R and data points show raw capture data (jittered for clarity), with blue data points representing surveys that detected the marbled cat at least once and red data points representing surveys that did not detect the marbled cat. Gray ribbons show the 95% confidence interval.

Wald's test is sensitive to a low sample size and there were only seven detections of marbled cats in degraded forests. Taken together, these results support our intuitive hypothesis that more arboreal nocturnal felids such as marbled cats are less adaptable to forest degradation and disturbances than their terrestrial and nocturnal relatives such as the leopard cat, jaguarundi, and ocelot, which are all commonly recorded in oil palm plantations (Jennings et al., 2015; Mendes-Oliveira et al., 2017; Pardo et al., 2021; Silmi et al., 2021).

Marbled cat habitat associations

At the regional scale, marbled cats were more likely to be found in areas with large forests, high forest cover, and high forest integrity, as measured by the FLII, largely concurring with existing literature (Haidir et al., 2021; Hearn et al., 2016, 2018). Previous surveys have failed to detect the marbled cat in oil palm plantations (Hearn et al., 2016, 2018; Jennings et al., 2015; Yue et al., 2015) and our models also suggest that the

TABLE 5 Variables associated with local (within site) marbled cat occupancy in Southeast Asia.

Predictor	Effect size	*K*	AIC_c	ΔAIC_c	AIC weight
Elevation	1.728	12	458.78	0	0.5611
Distance to river	0.590	12	464.48	5.7059	0.0324
Null	NA	11	466.91	8.1356	0.0096

Note: All hierarchical occupancy models included sampling effort as a covariate affecting detection probability and the camera trapping session as a covariate affecting occupancy. There were insufficient data for exploring multivariate models. Only predictors with AIC_c value smaller than the null model are included, with the direction of the effect sizes being positive for both predictors shown here (Figure 3d).

Abbreviations: AIC_c, corrected Akaike information criterion; NA, not applicable.

species is less abundant in forest habitats near to oil palm plantations. We failed to identify any significant predictor of marbled cat local occupancy, although there was weakly suggestive evidence for a positive effect of elevation, and this matches other work that finds marbled cats are more regularly detected at moderate to high elevation (relative to local maxima; Haidir et al., 2021; Hearn et al., 2018; Johnson et al., 2009; Pusparini et al., 2014; Sunarto et al., 2015). Although we note that Hearn et al. (2016) found some weak support for marbled cats preferring undisturbed lowland habitat compared with undisturbed high elevation forest. It is also important to note that the elevation range for the new camera trapping was relatively narrow (Appendix S1: Table S1), with the majority of surveys

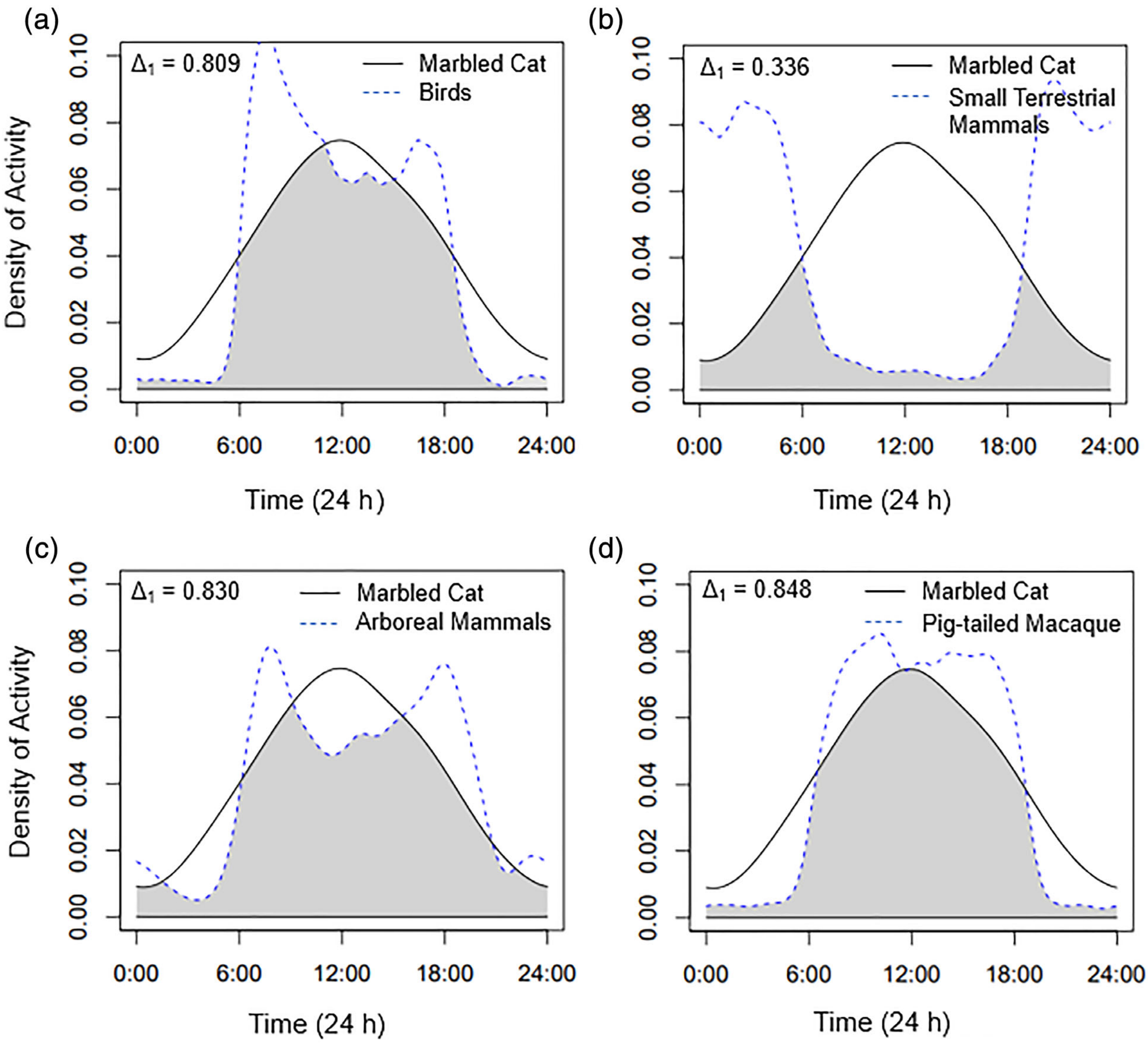

FIGURE 4 Diel activity pattern of the marbled cat and overlap with potential prey. Temporal overlap (Δ_1) between the marbled cat and (a) birds; (b) small terrestrial mammals (rats, mice, moonrats, and ground squirrels); (c) arboreal mammals (squirrels and tree shrews); and (d) the pig-tailed macaque.

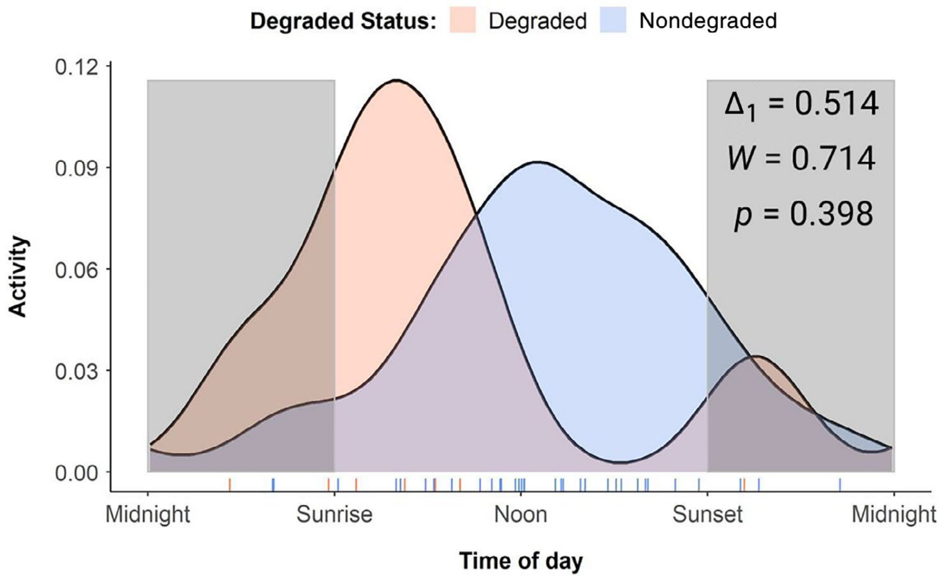

FIGURE 5 Diel activity pattern of the marbled cat in degraded and nondegraded forests. Time-stamped marbled cat detections were assigned to the degraded or nondegraded forest category based on whether the detection occurred in forest with a forest degradation value below or above the median value of the forest degradation variable of all marbled cat detections. Forest degradation was defined as the percent combined cover of oil palm plantations, lowland mosaic forest, lowland open ground, and regrowth forests within a 1.0-km radius of a camera trap in our new camera trapping sessions. Δ_1 refers to the extent of overlap in activity of marbled cats in the two different forest categories. *W* refers to the Wald test result comparing these two distributions and *p* refers to the *p* value associated with this Wald test.

conducted at elevations below 1000 m. This could have contributed to the non-significant result we observed.

Marbled cat ecology

We found that marbled cat's diurnal behavior has a higher temporal overlap with small, arboreal mammals and birds than with predominately nocturnal terrestrial small mammals (Figure 4; Appendix S1: Table S5). This supports other work suggesting that arboreal prey, such as squirrels, birds, and tree shrews, make up a larger proportion of the marbled cat's diet than ground-dwelling prey such as rats, mice, and moonrats (Lynam et al., 2013; Singh & Macdonald, 2017; Sunarto et al., 2015). Our results showed highest temporal overlap with pig-tailed macaques, and this concurs with Hearn et al. (2018), who identified that juvenile pig-tailed macaques as probable marbled cat prey. Pig-tailed macaques are known to forage in oil palm (Holzner et al., 2019; Ruppert et al., 2018) so the lack of suitable prey cannot explain the reduced detections of marbled cat nearby oil palm plantations.

Conservation implications

The marbled cat is currently listed as Near Threatened on the IUCN RL, as its global population is thought to be declining due to habitat loss and poaching (largely indiscriminate snaring) (Rasphone et al., 2021; Ross et al., 2016). This listing of Near Threatened is one of the lowest among Southeast Asian felids (Table 1). With only 18.5% of its 2015 IUCN RL range remaining as protected forest, we view that the marbled cat's conservation status is more comparable to that of other forest-dependent felids such as the clouded leopard (Vulnerable) than more disturbance-tolerant species such as the leopard cat (Least Concern). Further, given the marbled cat's avoidance of degraded forests (including edges and fragmented forests) and inability to adapt to oil palm landscapes, a population decline of more than 30% over the last 10-year period can be reasonably suspected. These threats have not ceased (Estoque et al., 2019; Grantham et al., 2020; Sasaki et al., 2021; Wilcove et al., 2013) so the marbled cat likely meets the requirements to be classified as Vulnerable under criterion A2 subsection C of the IUCN RL categories criteria (IUCN Standards and Petitions Committee, 2019). Conserving and increasing the connectivity of large intact forests is a priority for marbled cat conservation.

Directions for future research

Little is known about the marbled cat's arboreal behavior (Hearn et al., 2018). Further research on this topic may provide clarity on the marbled cat's need for tree connectivity and may be accomplished with movement tracking studies. Marbled cat movements and home range size also remain unclear since only a single individual has been successfully radio-tracked (Grassman et al., 2005) and there are only four published density estimates (Hearn et al., 2016; Naing et al., 2019; Rasphone et al., 2021; Singh & Macdonald, 2017). The varied patterns of the marbled cat's coat allow for individuals to be uniquely identified and make them good candidates for spatial capture–recapture studies. This has been an effective approach to study the ecologically similar margay in the neotropics (Harmsen et al., 2021).

CONCLUSION

Diurnal and arboreal felids may be at heightened risk from forest degradation and human activities than terrestrial and nocturnal counterparts, since they require canopy connectivity and have a reduced ability to temporarily avoid humans due to their diurnality. The conservation status of marbled cats and other semi-arboreal felids, such as the margay (Near Threatened), should also be reconsidered.

AUTHOR CONTRIBUTIONS

Matthew Scott Luskin designed the study. Matthew Scott Luskin and Jonathan H. Moore collected the data. Jonathan H. Moore, Zachary Amir, Calebe Pereira Mendes, and Matthew Scott Luskin prepared the data. Alexander Hendry, Zachary Amir, Adia Sovie, and Matthew Scott Luskin analyzed the data. Alexander Hendry and Matthew Scott Luskin wrote the paper, and all authors contributed to editing the final manuscript.

ACKNOWLEDGMENTS

We thank Yayasan Sabah, the Sabah Forest Department, the Sabah Biodiversity Council, and the Danum Valley Management Committee, Abdul Hamid, Glen Renolds, Jedediah Brodie, Katie Doehla, and Tombi Karolus for permission and help conducting fieldwork at Danum Valley. We thank the Smithsonian Institute and the Tropical Ecology Assessment and Monitoring (TEAM) network for collecting data from Pasoh, as well as Yao Tse Leong and the Forest Research Institute Malaysia (FRIM) for permissions to work at Pasoh. We thank Mohizah Bt. Mohamad, Januarie Kulis and the Sarawak Forestry Department for permission to conduct fieldwork at Lambir Hills. We thank NParks for permission and help with fieldwork in Singapore. We thank Wirong Chantorn, Anuttara Nathalang, Sarayudh Bunyavejchewin, Ronglarp Sukmasuang, Felise Gutierez, and Chris Scanlon for permissions and help at Khao Yai and Khao Ban Tat. In Sumatra, we thank Wido Rizqi Albert, Matthew Linkie, Yoan Dinata, Hariyo Wibisono, and HarimauKita for help facilitating fieldwork, and we thank Edi Siarenta Sembiring, Tarmizi and Eka Ramadiyanta, Salpayanri, Iswandri Tanjung, and Chris Decky for assistance with fieldwork. Original artwork was provided by courtesy of T. Barber from Talking Animals and is copyrighted. We thank the members of the Ecological Cascades Lab at the University of Queensland and two anonymous reviewers for comments that improved previous drafts.

FUNDING INFORMATION

The research was funded by the Smithsonian Institution's ForestGEO program, Nanyang Technological University in Singapore, the University of Queensland (UQ), National Geographic Society's Committee for the Research and Exploration award #9384-13 and Matthew Scott Luskin was supported by an Australian Research Council Discovery Early Career Researcher Award DECRA #DE210101440. In-kind support was provided by FFI, TEAM, WCS the Leuser International Foundation (LIF), and SEARRP.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Luskin et al., 2022) are available from Dryad: https://doi.org/10.5061/dryad.dz08kps09.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Hendry, Alexander, Zachary Amir, Henri Decoeur, Calebe Pereira Mendes, Jonathan H. Moore, Adia Sovie, and Matthew Scott Luskin. 2023. "Marbled Cats in Southeast Asia: Are Diurnal and Semi-Arboreal Felids at Greater Risk from Human Disturbances?" *Ecosphere* 14(1): e4338. https://doi.org/10.1002/ecs2.4338