Ecology, occurrence and distribution of wild felids in Sarawak, Malaysian Borneo

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Abstract Sarawak is the largest state in the megadiverse country of Malaysia. Its rich biodiversity is threatened by land-use change and hunting, with mammalian carnivores particularly affected. Data on the ecology, occurrence and distribution of small carnivores are crucial to inform their effective conservation, but no large-scale assessments have previously been conducted in Sarawak. Here we examine the status of the five species of felids in Sarawak based on data from camera-trap studies over 17 years (May 2003–February 2021) across 31 study areas, including protected areas of various sizes, production forests and forest matrix within oil palm plantations. Felids were detected at 39% of 845 camera stations. The marbled cat *Pardofelis marmorata* and Sunda clouded leopard *Neofelis diardi* had higher probabilities of occurrence in protected than unprotected areas, and vice versa for the leopard cat *Prionailurus bengalensis* and bay cat *Catopuma badia*. The marbled and bay cats were mostly diurnal, and the leopard cat was predominantly nocturnal; activity patterns did not substantively differ between protected and unprotected sites. The probabilities of occurrence of marbled and bay cats increased with greater distance from roads. The leopard cat and flat-headed cat *Prionailurus planiceps* were more likely, and the clouded leopard less likely, to occur near rivers. Flat-headed cats preferred peat swamp forest, bay cats lowland forest, and marbled cats and clouded leopards occurred in both lowland and montane forest. Felids may tolerate higher elevations to avoid anthropogenic disturbance; therefore, it is critical to preserve lowland and mid-elevation habitats that provide refugia from climate change and the destruction of lowland habitat.

Keywords Felids, fragmentation, habitat loss, land-use change, logging, occurrence, oil palm, protected area

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Introduction

Located in a global biodiversity hotspot, Sarawak, the largest state in Malaysia, has high species diversity and endemism, but this biodiversity is threatened by intense anthropogenic impacts (Ling & Julia, 2012; Hon & Shibata, 2013; Mathai et al., 2016) such as rapid land-use change (Wilcove & Koh, 2010). The expansion of oil palm plantations and logging operations, for example, has reduced natural habitats for many species of conservation concern (Mathai et al., 2010, 2016; Gerber et al., 2012; Hon & Shibata, 2013; Runting et al., 2015; Caruso et al., 2016). The average deforestation rate in Borneo is c. 0.25 million ha annually (Gaveau et al., 2019) and Sarawak lost c. 80% of its primary forest during 1973–2015 (Gaveau et al., 2016). In addition, the development of roads has increased access into previously remote areas, facilitating hunting and other extractive activities. Although hunters in Borneo do not usually target felids, they may take them opportunistically (Kerley et al., 2003; Brodie et al., 2015b; Mohd-Azlan et al., 2017), and larger felid species may be affected by hunting-induced prey depletion. Hunting poses a greater long-term threat than logging to 91% of Bornean primates and ungulates because hunters continue to operate even in overexploited areas (Brodie et al., 2015b). The decline of carnivores can have cascading effects on ecosystems, as they can be important for regulating prey populations or dispersing plant seeds (Mathai et al., 2010; but see Brodie & Giordano, 2013).

Felids are often regarded as charismatic flagship species that can be used to highlight the conservation value of an area. However, little is known about the distribution and ecology of many felids in Sarawak. This scarcity of information on the ecological needs of felids poses a challenge for conservation planning in the state. Five wild felid species occur in Sarawak: the relatively large Sunda clouded leopard *Neofelis diardi* (11–25 kg), the medium-sized Bornean bay cat *Catopuma badia* (also referred to as *Pardofelis badia*; 3–5 kg) and marbled cat *Pardofelis marmorata* (2.5–5 kg),

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and the smaller leopard cat *Prionailurus bengalensis* (2–2.5 kg) and flat-headed cat *Prionailurus planiceps* (1.5–2.5 kg; Wilting et al., 2007; Phillipps & Phillipps, 2016). The leopard cat is listed as Protected and the other species as Totally Protected under the Sarawak Wild Life Protection Ordinance of 1998. Offences involving a Protected or Totally Protected species can result in imprisonment for 1 or 2 years and fines of MYR 10,000–25,000, respectively. The bay and flat-headed cats are categorized as Endangered on the IUCN Red List, the clouded leopard as Vulnerable, the marbled cat as Near Threatened and the leopard cat as Least Concern (IUCN, 2021). Lack of information on these cryptic species is hampering conservation planning in the changing landscapes of Sarawak.

Bornean felids are distributed across a broad range of forest types: lowland mixed dipterocarp, mangrove, peat swamp and montane forest (Wilting & Fickel, 2012; Jennings et al., 2013; Mohamed et al., 2013). Some also occur in human-modified habitats such as plantations, logged forests, orchards or urban areas (Gehring & Swihart, 2003; Meijaard & Sheil, 2008; Mohamed et al., 2013; Jennings et al., 2015). Bornean felids differ in their spatial and temporal habitat use (Hearn et al., 2018). Here we report extensive data on Bornean felids from camera-trap surveys over 17 years in 31 study areas across Sarawak to (1) describe spatio-temporal occurrence patterns, (2) update data on the distribution of felids in the state, and (3) determine the occurrence probabilities of felids based on protected area status, habitat type, and other anthropogenic and ecological variables.

Study area

Sarawak has a total area of c. 124,450 km^2, with c. 79% covered by various types of forests (intact, degraded, mangrove and peat swamp forests); c. 21% of the state is agricultural land or plantation (Bryan et al., 2013; Gaveau et al., 2014). We conducted camera-trap surveys intermittently during May 2003–February 2020 in 31 study areas (Supplementary Table 1) across Sarawak. Study sites included 24 protected areas (21 national parks, two wildlife sanctuaries and one nature reserve) and seven unprotected areas (two highland areas, four production forests and one oil palm plantation–forest matrix; Fig. 1). Many of the protected areas in the state (including some of those included in this study) are small, fragmented and surrounded by human settlements, agricultural plantations or logging concessions (Mathai et al., 2010; Hon & Shibata, 2013). Most of the protected areas were more easily accessible than some of the unprotected sites, which were remote and/or accessible only by private, guarded logging roads. The main ethnic groups in the study area in Sarawak are the Iban, Bidayuh, Kenyah, Kayan and Penan peoples, many of whom depend on wildlife hunting for subsistence. Study areas were dominated by mixed dipterocarp forest, followed by peat swamp, heath (called *kerangas* locally), mangrove, montane, beach and riverine forests (Hazebroek & bin Abang Morshidi, 2000; Gaveau et al., 2014).

Methods

Data collection

We deployed a total of 861 camera stations across the 31 study areas, with usable data obtained from 845 units. Cameras were deployed singly and were operational continuously. We standardized camera-trap deployment across all study sites, following Mohd-Azlan & Engkamat (2013) and Brodie et al. (2015b). We secured camera traps (RM45, Reconyx, Holmen, USA, and TrophyCam, Bushnell, Overland Park, USA) to trees, at a height of 30–70 cm above the ground for optimal detection of mammals across a range of body sizes. Cameras were faced away from direct sunlight to prevent false triggers. Camera traps were usually positioned on animal trails or pathways, or near natural salt licks, and spaced at least 1 km apart. They were set to take three burst shots when triggered, followed by a quiet period of 1–2 minutes before the next trigger, to reduce the likelihood of capturing the same individual repeatedly. To ensure independence of captures, we only retained records of the same species at a given station that were at least 1 hour apart.

Analysis of activity patterns

We structured, analysed and visualized species-specific activity patterns using the packages *camtrapR* (Niedballa et al., 2016) and *overlap* (Ridout & Linkie, 2009) in *R 4.0.3* (R Core Team, 2020). We assumed the relative frequency of captures at different times of day to be related to the animals' activity patterns (Kawanishi, 2002; Mohd-Azlan, 2006), and considered species diurnal when recorded during 6.00–18.00 and nocturnal when recorded during 18.00–6.00. We used a kernel density estimator to assess the area under the distribution curves of two sympatric species, where Δ is the actual coefficient of overlap:

$$\Delta(f, g) = \int \min\{f(x),\ g(x)\}\mathrm{d}x \qquad 1$$

where f(x) and g(x) are the density distributions of detection times for each species. Subsequently, we used the $\hat{\Delta}_1$ estimator to compare activity overlap (Ridout & Linkie, 2009).

Analysis of species occurrence

We determined how the occurrence of species was related to four ecological and anthropogenic factors: elevation (m) and the distances (m) to the nearest road, river or longhouse as measured with a GPS and/or a GIS with satellite imagery.

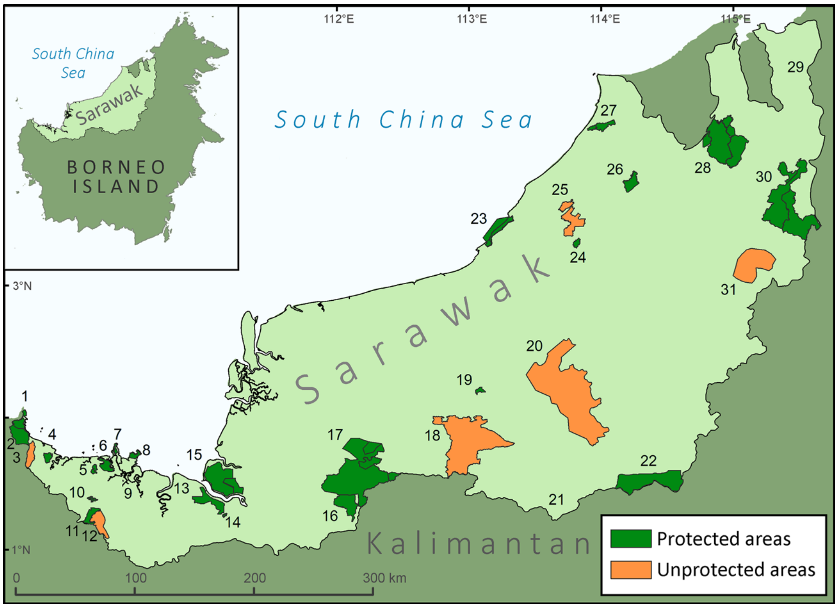

FIG. 1 Locations of the 31 study areas in Sarawak covering both protected and unprotected areas. (1) Tanjung Datu National Park, (2) Samunsam Wildlife Sanctuary, (3) Gunung Pueh National Park, (4) Gunung Gading National Park, (5) Kubah National Park, (6) Kuching Wetland National Park, (7) Santubong National Park, (8) Bako National Park, (9) Sama Jaya Nature Reserve, (10) Dered Krian National Park, (11) Bungoh Range National Park, (12) Gunung Penrissen, (13) Ulu Sebuyau National Park, (14) Gunung Lesung National Park, (15) Maludam National Park, (16) Batang Ai National Park, (17) Lanjak Entimau Wildlife Sanctuary, (18) Ulu Kapit Forest Mangement Unit, (19) Pelagus National Park, (20) Hose Mountain, (21) Ulu Baleh, (22) Baleh National Park, (23) Similajau National Park, (24) Sungai Meluang National Park, (25) Oil Palm Plantation matrix, (26) Loagan Bunut National Park, (27) Lambir Hills National Park, (28) Gunung Mulu National Park, (29) Ulu Trusan, (30) Pulong Tau National Park, (31) Baram.

Native peoples still live and hunt in Sarawak as they have for millennia, with the whole community of a village occupying a single longhouse. We assumed the intensity of anthropogenic activities would be greatest near a longhouse and thus measured the distance from a camera trap to the nearest longhouse as an indicator of the intensity of anthropogenic disturbance that could influence species distributions. Occurrence probabilities were estimated using the Dorazio–Royle community model (Kéry & Royle, 2015; Huang et al., 2020). This hierarchical model assesses responses to ecological and anthropogenic factors based on the suite of detection histories across the species community (Brodie et al., 2015b; Kéry & Royle, 2015; Huang et al., 2020). It can overcome errors stemming from unequal sampling efforts and produce reliable and precise results that accommodate imperfect detections (Dorazio & Rodriguez, 2012; Taylor-Rodriguez et al., 2017). The model was therefore suitable for investigating a community of species that differed in their probabilities of occurrence and detection. We divided camera-trap data into 7-day sampling occasions ($N = 277$; Bisi et al., 2019). The responses of each species to the covariates were determined through mean and variance hyperparameters. We treated the original detection histories of species k at site i during occasion j (y_{ijk}) as Bernoulli random variables:

$$\begin{aligned}\mathrm{Logit}(\Psi_{ik}) = {} & \Psi_k + \mathrm{B}l(\Psi_k) \times \mathrm{elevation}_i + \mathrm{B}l(\Psi_{2k}) \\ & \times \mathrm{longhouse}_i + \mathrm{B}l(\Psi_{3k}) \times \mathrm{road}_i \\ & + \mathrm{B}l(\Psi_{4k}) \times \mathrm{river}_i \qquad (2)\end{aligned}$$

where B denotes estimated coefficients and $l(\Psi_k)$ are the logit occupancies of species k.

We ran seven chains with 100,000 iterations for the Dorazio–Royle community model after a burn-in of 5,000. We generated 89% credible intervals as these have been suggested to be more stable than 95% credible intervals when sample sizes are $< 10{,}000$ (Huang et al., 2020). We predicted species occurrence as a function of covariates when there was a significant relationship ($P < 0.05$) between them. We then applied the estimated linear model parameters with identical scaling to calculate predictions, using three chains with 22,000 iterations after a burn-in of 2,000. We plotted the 6,000 posterior summaries of the predictions for each species into a single array against the original (i.e. unscaled) values of the covariate.

Analysis of species distributions

We assessed species distribution using occurrence coordinates (presence data only) of felids, which were pooled and overlain with GIS layers of habitat type to assess suitable areas for each felid species. We obtained the GIS layer for terrestrial ecoregions from The Nature Conservancy (TNC, 2020) and defined five habitat types: (1) lowland forest, (2) lower montane forest, (3) peat swamp forest, (4) mangrove forest and (5) tropical heath forest. We did not assess oil palm plantations as potential parts of species ranges. The GIS layers were categorized and clipped with the Sarawak map to a cell size of c. 1 km² (Jennings et al., 2013). We used the occurrence data and clipped environmental layers to model the distribution of all species using maximum entropy with a jackknife analysis in *MaxEnt 3.4.1* (Phillips et al., 2017). *MaxEnt* assesses the distribution probability of the maximum entropy of target species by inferring the occurrence data even with incomplete information (Phillips et al., 2006; Elith et al., 2011).

Results

Detections in protected and unprotected sites

We identified 3,545 photographs of felids from a total of 2,628,993 images (c. 0.1%); 863 of these were independent captures. Among the five felids, the highest number of independent captures was of the leopard cat (681), followed by the marbled cat (94), clouded leopard (56), Bornean bay cat (21) and flat-headed cat (11; Supplementary Table 2). Felids were detected at 332 of 845 camera stations (39.3%). The leopard cat was detected most often (85 stations in protected and 141 in unprotected areas), followed by the marbled cat (23 stations each in protected and unprotected areas), clouded leopard (21 stations in protected and 14 in unprotected areas), bay cat (eight stations in protected and 13 in unprotected areas) and flat-headed cat (six stations in protected areas).

Felids were detected in 26 of the 31 study areas (83.9%; 19 protected and seven unprotected sites with at least one species; Supplementary Table 2). We did not detect any felids in Samunsam Wildlife Sanctuary, Sama Jaya Forest Reserve, and Kuching Wetland, Maludam and Similajau National Parks. In none of the study sites did we record all five Bornean felids. Four felids (all except the flat-headed cat, a wetland specialist) were recorded in two unprotected areas (Kapit and Baram). The flat-headed cat was recorded in only two protected peat swamp forests (Loagan Bunut and Ulu Sebuyau National Parks). Cameras in six sites recorded the leopard cat only: Bako, Bungoh Range, Dered Krian, Santubong and Tanjung Datu National Parks and Ulu Trusan. In Sungai Meluang National Park only the marbled cat was recorded. The bay cat was detected at nine study sites (29.0% of the total), with no more than two independent photographs per site, except in Kapit, where there were 11 independent detections. The largest felid, the clouded leopard, was detected in nine study areas (29.0% of the total), with the highest number of independent detections (N = 19) in Pulong Tau National Park (Supplementary Table 2). The leopard cat was detected at the highest percentage of study sites (32.9% of locations), followed by bay cat (28.3%), marbled cat (10.7%), clouded leopard (10.6%), and flat-headed cat (4.6%; Fig. 2). The marbled cat and clouded leopard had higher probabilities of occurrence in protected than unprotected areas, and vice versa for the leopard cat and bay cat (Fig. 2).

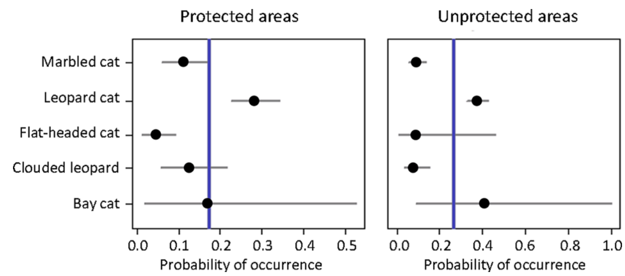

Fig. 2 Estimated probabilities of occurrence of the five felid species in Sarawak in protected and unprotected study areas. Black points indicate mean occurrence, horizontal lines show the interquartile range, and vertical lines indicate the mean occurrence of all species.

Activity patterns

The marbled and bay cats were mostly diurnal, and the leopard cat was predominantly nocturnal. The clouded leopard and flat-headed cat were cathemeral, although clouded leopard activity was mostly at night, with only few captures during the day, and the small number of flat-headed cat detections (N = 11) peaked around midnight (Fig. 3). Except for the flat-headed cat, which was only recorded in protected areas, activity patterns for the felids did not differ substantively between protected and unprotected study sites, with activity overlap ranging from $\hat{\Delta}_1$ = 0.61 to 0.80 (Fig. 3).

Occurrence patterns

Although the detection rates of all species except the leopard cat were relatively low, we found some statistically significant associations between habitat variables and species occurrence. The occurrence of the marbled (mean model coefficient = 1.60, 89% CI = 0.51, 2.92) and bay cats (mean = 2.50, 89% CI = 0.92, 4.65) increased at greater distances from the nearest road (Figs 4 & 5a). The occurrence of the leopard cat (mean = 6.03, 89% CI = 2.29, 10.04), flat-headed cat (mean = −5.94, 89% CI = −12.61, 0.00) and clouded leopard (mean = −6.30, 89% CI = −10.85, −1.98) were significantly affected by distance to river (Fig. 4). Leopard cats and flat-headed cats were more likely to occur near rivers, whereas clouded leopards were more likely to occur away from rivers (Fig. 5b). Elevation influenced the occurrence of the flat-headed cat (mean = −5.47, 89% CI = −10.98, −1.33) and clouded leopard (mean = 1.49, 89% CI = 0.81, 2.29; Fig. 4), with flat-headed cats having a higher probability of occurrence at low elevation and the probability of occurrence of the clouded leopard increasing slightly above 900 m (Fig. 5c). The occurrence of none of the felids was affected by the distance to the nearest longhouse (mean = 0.11, 89% CI = −1.44, −1.70).

Except for the flat-headed cat, Bornean felids were distributed across a relatively wide range of elevations (up to and above 1,000 m; Fig. 6). The flat-headed cat

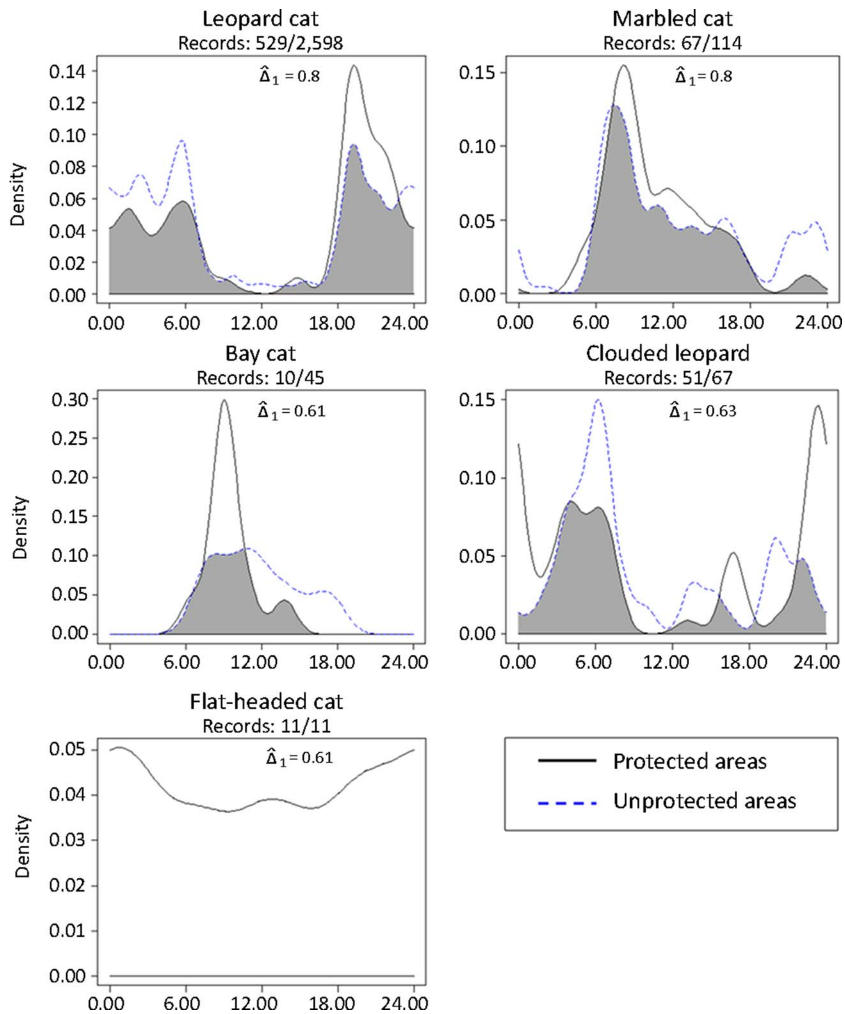

FIG. 3 Diel activity patterns of five felid species in Sarawak and the degree of overlap ($\hat{\Delta}_1$ =) between protected and unprotected study areas. Note the different scales of the y-axes. The number of records indicates the total number of photographs used in the analysis, given as separate totals for protected/unprotected areas.

appears to be restricted to lowland forest, with most records from below 100 m. Most detections of the leopard cat and bay cat were below 700 m, whereas the probability of occurrence of the marbled cat increased above 700 m (Fig. 6).

Species distributions

Based on *MaxEnt* modelling, flat-headed cats preferred peat swamp forest, marbled cats and clouded leopards preferred both lowland and montane forest, bay cats generally preferred lowland forest, and leopard cats did not exhibit any preference for particular habitat types.

Discussion

Our study describes the distribution and occurrence patterns of felids as assessed over 17 years and across 31 localities in Sarawak, relative to ecological and anthropogenic variables. Bay and leopard cats had higher occurrence probabilities in unprotected than in protected sites in Sarawak. Leopard cats were previously known to have a high tolerance, and possible preference, for certain human-modified landscapes. Previous research suggested that unprotected areas such as plantations and agricultural areas, which often harbour rodents in high abundance, can sustain a high density of leopard cats, which exploit rodents as their main prey (Rajaratnam, 2000; Jennings et al., 2015; Chua et al., 2016). This is consistent with our findings: leopard cats were mostly recorded in oil palm plantation–forest matrix (Supplementary Table 2). The highest occurrence of leopard cats (Ψ = 0.797) was in the unprotected Gunung Penrissen, which is surrounded by settlements, plantations and fruit orchards (Jayaraj et al., 2006; Kaicheen & Mohd-Azlan, 2018; Supplementary Table 2). Within protected areas, the probability of occurrence was highest (Ψ = 0.773) in the isolated Gunung Gading National Park, surrounded by oil palm plantations and rural settlements (Arif & Mohd-Azlan, 2014). Bay cats were recorded at six protected sites, with a low total number of independent captures (Supplementary Table 2). The occurrence probability of the bay cat appeared to be higher at unprotected study

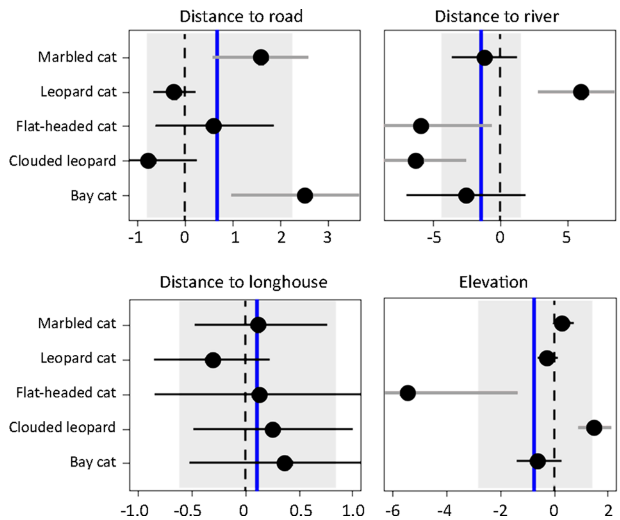

FIG. 4 The influence of elevation and distance from road, river and longhouse on occupancy of felid species in Sarawak. Black dots indicate the occupancy model coefficient for each species, black horizontal lines the 89% Bayesian credible intervals. Grey horizontal lines indicate significance. Vertical lines and shaded areas show the mean and 89% Bayesian credible intervals for community-level estimates, respectively. Vertical dashed lines show the zero-effect size.

sites ($\Psi = 0.411$) than in protected areas ($\Psi = 0.155$), with most of the captures in Ulu Kapit, central Sarawak, a logging concession; although not officially protected, this area contains large tracts of continuous lowland forest, which could be one of the reasons for the relatively high occurrence of bay cats there. Past studies have also recorded this species in production forests such as Sela'an Linau Forest Management Unit (Mathai et al., 2014) and Muput Forest Management Unit (Hon, 2011) in Sarawak, several sites in Sabah (Wearn et al., 2013; Hearn et al., 2018) and East Kalimantan (Sastramidjaja et al., 2015). Our findings confirm that production forests, as part of a landscape that also contains large areas of intact forest, can contribute to sustaining species of conservation importance.

Our data corroborate the findings of previous studies suggesting that felids exhibit diel activity patterns ranging from strongly nocturnal to largely diurnal. The activity patterns of the clouded leopard, and the marbled, bay and leopard cats, were consistent with those observed by Hearn et al. (2018), with marbled and bay cats being diurnal, clouded leopard cathemeral and leopard cat nocturnal with minimal activity after dawn or before dusk (Fig. 3). The diel activity of the flat-headed cat in our study was consistent with that observed by Adul et al. (2015) in central Kalimantan (Fig. 3); the species is nocturnal and is often detected during surveys by boat at night (Hearn et al., 2010; Mohd-Azlan & Thaqifah, 2020). Temporal activity rhythms of larger tropical mammals can be shaped by habitat degradation and other anthropogenic activities (Norris et al., 2010), and thus reflect the tolerance of particular species to forest disturbance (Griffiths & Schaik, 1993; Norris et al., 2010). We detected differences in activity patterns between protected and unprotected areas for some species, but these differences were small. Likewise, Bernard et al. (2013) found no impact of anthropogenic activities on the activity patterns of a suite of mammals in Imbak Canyon Conservation Area, Sabah.

Lowland dipterocarp forest appears to be the preferred habitat type of the felids in Sarawak, with the exception of the flat-headed cat. Felids appear to be widely distributed along elevation gradients up to 1,700 m. The flat-headed cat is closely associated with water bodies and usually only recorded in lowland areas (Bezuijen, 2000; Cheyne et al., 2009; Hearn et al., 2010; Wilting et al., 2010, 2016; Wadey et al., 2014; Mohd-Azlan & Thaqifah, 2020), although the species has been detected at elevations of up to 780 m in Sabah (Brodie & Giordano, 2011). Consistent with this, most detections of the flat-headed cat in our study were along riverbanks; multi-species occurrence models showed the effects of river proximity (positive) and elevation (negative) on flat-headed cat occurrence (Fig. 4).

Elevation is often used as a proxy for changes in habitat characteristics, such as decreasing temperature and changing forest stature from lowlands to highlands (with associated transitions in plant species composition); there are also probably changes in the density of prey for carnivores (Mohamad et al., 2015). Felids and other medium-sized and large lowland animals may use higher elevations to avoid anthropogenic activities (Tan et al., 2017); it is therefore critical to preserve mid-elevation habitats as refugia from lowland habitat destruction and climate change (Brodie, 2016; Brodie et al., 2017; Scriven et al., 2020; Williams et al., 2020). Wetlands, including peat swamp forest, are also important sites for conserving felids and numerous other species, despite frequently being considered wastelands deficient in nutrients and low in species diversity (JM-A, pers. obs., 2021). Wetlands have received relatively little conservation attention in Sarawak and many have been converted to other land uses (Yule, 2010; Posa et al., 2011; Tsuyuki et al., 2011). A previous study reported that the bay cat was associated with rivers (Mohd-Azlan & Sanderson, 2007). However, we found the occurrence of bay cats was not closely associated with rivers, but rather influenced by roads; occurrence of this species increased > 10 km from roads (Figs 4 & 5a). This species also appears to be distributed mostly at intermediate elevations, consistent with the findings of Hearn et al. (2018), although it has been detected as high as 1,460 m in Pulong Tau National Park, Sarawak (Brodie & Giordano, 2012). Similar to the bay cat, the occurrence of the marbled cat increased sharply at distances of > 25 km from roads (Fig. 5a). Occurrence of the clouded leopard appeared to be associated with rivers and elevation (Figs 4 & 5c), but not with roads. This is in

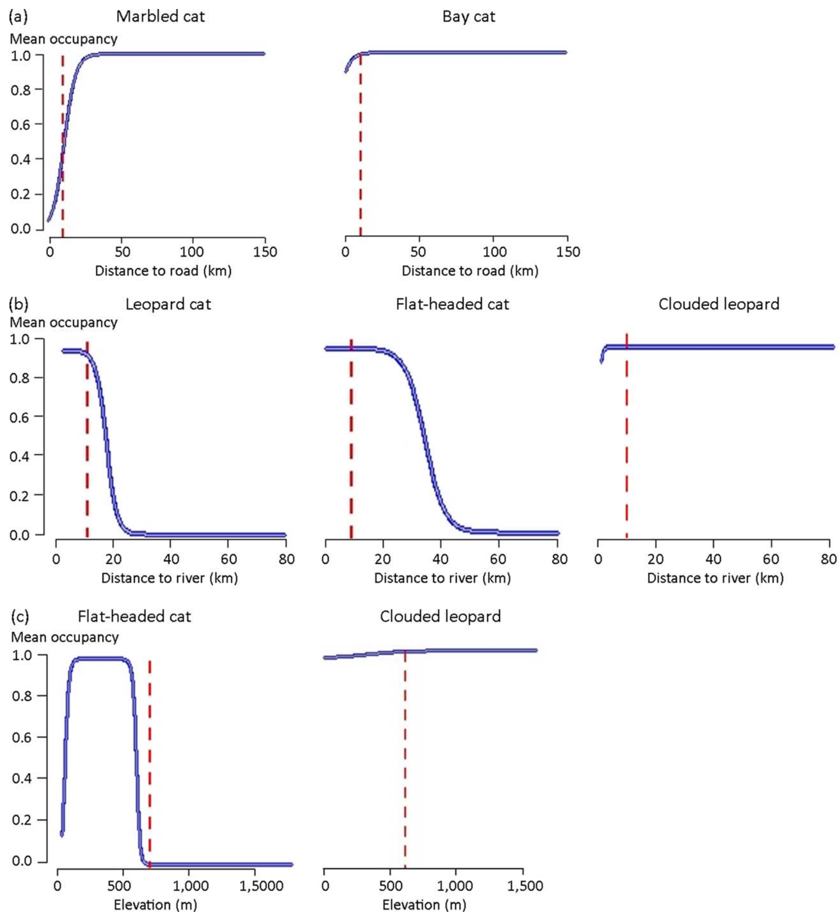

FIG. 5 (a) Predicted occurrence probabilities of marbled cat and bay cat in Sarawak in relation to the distance to the nearest road; dashed vertical lines indicate 10 km. (b) Predicted occurrence probability of leopard cat, flat-headed cat and clouded leopard in relation to the distance to the nearest river; dashed vertical lines indicate 10 km. (c) Predicted occurrence probability of flat-headed cat and clouded leopard in relation to elevation; dashed vertical lines indicate 700 m (the approximate transition between lowland and lower montane forest).

contrast to previous research in Sabah suggesting that male (but not female) clouded leopards may preferentially utilize roads for travel (Wearn et al., 2013; Hearn et al., 2018); the difference could stem from a higher hunting pressure in Sarawak than in Sabah, reducing selection for areas such as roads that are frequented by people. Previous research also suggested that the local abundance of the clouded leopard declines in areas with high road density (Brodie et al., 2015a), that elevation affects the distribution of this species, and that it is tolerant of logging concessions but not oil palm plantations or coastal regions (Brodie et al., 2015a; Yue et al., 2015; Hearn et al., 2016).

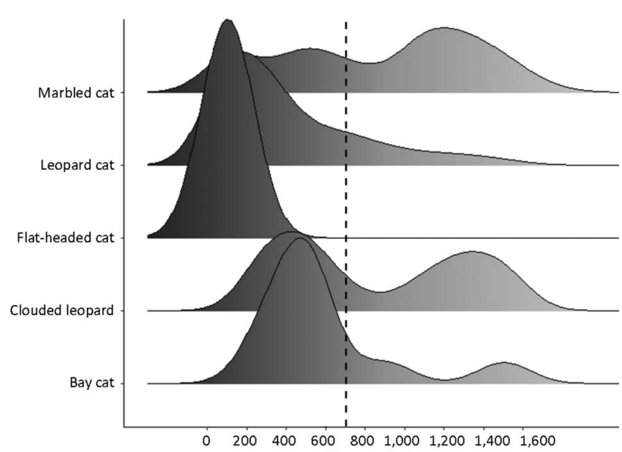

FIG. 6 Ridgeline plots illustrating the relative frequency of independent detections as functions of elevation; the dashed vertical line at 700 m denotes the approximate transition between lowland and lower montane forest. Maximum absolute frequency of detections varied from 11 (flat-headed cat) to 681 independent detections (leopard cat).

Most protected areas in Sarawak are relatively small and surrounded by human-dominated areas, a fact that should be considered when determining the conservation value of existing and prospective protected areas for the long-term viability of felids and other species in the state. Maintaining a connected network of forests, even if some of the areas are degraded or partly used for wood or fibre production, is important for species conservation in this increasingly changing landscape (Brodie et al., 2016). The development of effective conservation plans for felids in Sarawak will depend on the determination of realistic and achievable targets, an appreciation of the particular conservation and environmental contexts in the state, and reliable data on local species distributions and ecology, as presented here.

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Ethical standards This research abided by the *Oryx* guidelines on ethical standards, followed protocols of the permitting agencies and universities, and did not involve human subjects, experimentation with animals or collection of biological specimens.

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