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Assessing the distribution and habitat use of four felid species in Bukit Barisan Selatan National Park, Sumatra, Indonesia

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ABSTRACT

There have been few targeted studies of small felids in Sumatra and there is little information on their ecology. As a result there are no specific management plans for the species on Sumatra. We examined data from a long-term camera trapping effort, and used Maximum Entropy Modeling to assess the habitat use and distribution of Sunda clouded leopards (Neofelis diardi), Asiatic golden cats (Pardofelis temminckii), leopard cats (Prionailurus bengalensis), and marbled cats (Pardofelis marmorata) in Bukit Barisan Selatan National Park. Over a period of 34,166 trap nights there were low photo rates (photo events/100 trap nights) for all species; 0.30 for golden cats, 0.15 for clouded leopards, 0.10 for marbled cats, and 0.08 for leopard cats. There is overlap in the predicted distributions of clouded leopards, golden cats, and marbled cats; indicating areas of high conservation importance for these species within the park. The predicted distribution of leopard cats was discrete from the other species which is important to consider in the development of conservation strategies. This study provides important documentation of small felid distribution in Sumatra, information for the development of management strategies within the park, and a basis upon which to develop future research for the species.

1. Introduction

As habitat degradation and loss increasingly threaten Sumatran wildlife, it has become imperative to assess the habitat use and distribution of species in order to prioritize critical areas for protection. Sumatra is home to six wild felid species: the leopard cat (*Prionailurus bengalensis*), the Sunda clouded leopard (*Neofelis diardi*), the marbled cat (*Pardofelis marmorata*), the Asiatic golden cat (*Pardofelis temminckii*), the flat-headed cat (*Prionailurus planiceps*), and the Sumatran tiger (*Panthera tigris sumatrae*). Currently, only the leopard cat is not considered either threatened or endangered (IUCN, 2011). The Sunda clouded leopard population has already been designated as a separate species from the mainland population and a species level distinction has recently been proposed for the Sunda leopard cat and marbled cat as well (Buckley-Beason et al., 2006; Kitchener et al., 2006; Wilting et al., 2007; Christiansen, 2008; Wilting et al., 2011; Luo et al., 2014). While there have been several studies focused on the Sumatran tiger (e.g. Linkie et al., 2003; Nyhus and Tilson, 2004; Linkie et al., 2006; Wibisono and Pusparini, 2010; Wibisono et al., 2011), there have been few studies of the other felid species on Sumatra, and little

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is known of their ecology, habitat use, distribution or status on the island (Sollman et al., 2014; Pusparini et al., 2014). Currently, the majority of information on the species is taken from studies occurring on Borneo or in mainland Southeast Asia (Rabinowitz, 1990; Grassman and Tewes, 2002; Grassman et al., 2005a,b; Austin et al., 2007; Rajaratnam et al., 2007; Kawanishi and Sunquist, 2008; Ghimirey and Pal, 2009; Cheyne and MacDonald, 2011; Brodie and Giordano, 2012; Wilting et al., 2012; Mohamed et al., 2013; Cheyne et al., 2013; Hearn et al., 2013). However, even in these areas there is an overall paucity of information, with a general lack of data often limiting the potential to infer habitat preference and distribution, much less prescribe conservation measures, for these rare and elusive species.

The use of remote cameras has become an important tool in wildlife research, particularly for the study of cryptic or rare species. Recently, data from camera trap photographs have been used in ecological niche models in order to predict species distribution (Monterroso et al., 2009; Wilting et al., 2010; Jenks et al., 2012; Torres et al., 2012). Such models are important for a variety of applications (Graham et al., 2004; Peterson et al., 2007), but may be particularly useful in the identification of critical habitat for threatened and endangered species. However, by nature, there is a paucity of data for these rare species and the datasets often consist of zero inflated or presence-only data. Thus, any model employed must be able to make accurate predictions from a small amount of information. Several different presence-only modeling techniques have been effectively used for this purpose, including ecological niche factor analysis, Genetic Algorithm for Rule-set Production (GARP), and Maximum Entropy Modeling (Maxent) (Stockwell and Peters, 1999; Hirzel et al., 2002; Hernandez et al., 2006; Philips et al., 2006; Kumar and Stohlgren, 2009; Rebelo and Jones, 2010). The use of models that utilize only presence data has been debated, but recent studies have shown that in some cases, presence-only modeling techniques may even have a better predictive accuracy than more traditional presence–absence methods (Elith et al., 2006; Cianfrani et al., 2010).

Here we use MaxEnt to model the habitat use and distribution of four Sumatran felids (Sunda clouded leopard, marbled cat, Asiatic golden cat, and leopard cat) in Bukit Barisan Selatan National Park (BBSNP). We then use the results to identify areas of high conservation priority for the conservation of felids within BBSNP. The data from this research will be beneficial as a basis for studies elsewhere on the island and to aid in the development of an island-wide conservation plan for the species.

2. Study area

Located in southwestern Sumatra, BBSNP is the third largest protected area in Sumatra with a total area of 3568 km^2. It was established as a national park in 1982, and is part of the UNESCO World Heritage Site, Tropical Rainforest Heritage of Sumatra. BBSNP contains some of the largest tracts of lowland tropical rainforest remaining in Sumatra and is a major watershed for the southwestern region of the island. The park extends 150 km along the Bukit Barisan mountain range with a diverse topography ranging from coastline in the south to mountainous forest in the north. It was designated as a Priority III conservation area for the Sumatran tiger (Dinerstein et al., 2006), and provides critical habitat for other endangered species such as the Sumatran rhino (*Dicerorhinus sumatrensis*), the Sumatran striped rabbit (*Nesolagus netscheri*), and the Sumatran elephant (*Elephas maximus sumatrensis*) (Wibisono, 2005; McCarthy et al., 2012). The park is bordered by dense clusters of villages, agricultural fields, and oil palm plantations, and has experienced significant levels of deforestation since its establishment. In 1977, record high prices for robusta coffee caused an influx of small-scale coffee farmers to mountainous areas in and around BBSNP (Gaveau et al., 2009). Since then, agricultural expansion for coffee production has been the dominant driver of deforestation inside the park (Suyanto, 2007; Gaveau et al., 2009), with an estimated loss of 57,344 ha of forest between 1972 and 2002 (Gaveau et al., 2007).

3. Methods

We conducted surveys in BBSNP between 1998 and 2011 using both film (CamTrakker, Watkinsville, Georgia, USA 30677) and digital (Reconyx HC500, Holmen, Wisconsin, USA) remote cameras. Both types of camera were set to operate continuously, using either flash or infrared photography at night. Although we must acknowledge possible differences in trigger sensitivity between the film and digital cameras, we did not detect any trap shyness in response to the use of visible flashes (Gibeau and McTavish, 2009), and photo rate was comparable between both types of camera. Cameras automatically recorded the date and time for each photograph. The film cameras took a single photograph per triggering event and were set to delay sequential photographs for 45 s. The digital cameras were set to take a series of five photographs per triggering event, with a 60-s delay between sequential triggers.

Cameras were set according to O'Brien et al. (2003) for the duration of the study. They were placed within sampling blocks which were spaced regularly from the north of the park to the south at 10- to 15-km intervals, and additional cameras were placed in a comprehensive grid across the southern end of the park (Fig. 1). Each sampling block was divided into 20, 1-km^2 subunits, and a random UTM coordinate was located within each subunit. Cameras were placed within 100 m of the UTM coordinate at the most optimal location for obtaining photographs of vertebrates. Optimal camera locations were typically on animal trails that showed sign of recent activity. Cameras were mounted on tree trunks so that the infrared beam was between 25 and 45 cm above the forest floor. Cameras were deployed in the forest for 30–35 days before being retrieved and moved to a new UTM coordinate within the subunit, or in some cases the batteries were changed and the camera remained in place. The number of trap nights for each camera was defined as the period beginning with its deployment until it was

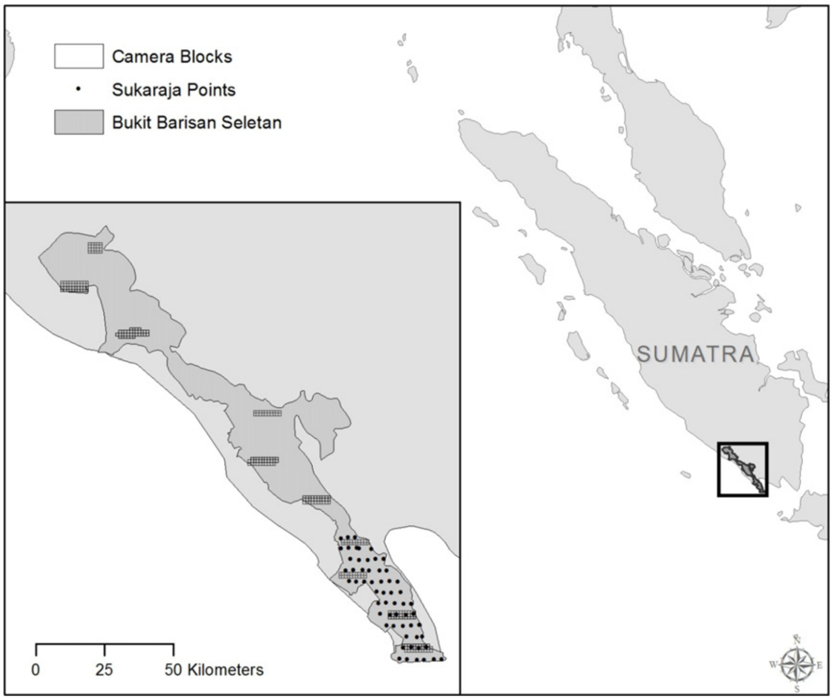

Fig. 1. Camera locations within Bukit Barisan Selatan National Park. Camera blocks indicate sampling sites where cameras were placed at different random UTMs within a 1 km^2 block. The Sukaraja points represent a comprehensive grid of camera points across the southern portion of the park.

retrieved, if the film had exposures remaining, or until the time and date stamped on the final exposure. Each photograph of an animal was identified to species, and if the quality of the photograph did not allow an absolute identification the photograph was excluded from the dataset. Sequential frames of the same species were counted as one photographic event, and unless individual identification was possible, any subsequent photograph of the same species taken within 30 min of the first was not considered a new photographic event.

The location of each felid photograph was recorded by latitude and longitude, and identified to species. Land cover data for Southeast Asia was downloaded from Global Land Cover 2000 (GLC 2000; Global Land Cover 2000 database. European Commission, Joint Research Centre, 2003. http://bioval.jrc.ec.europa.eu/products/glc2000/glc2000.php). Six climatic variables (annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the wettest month, precipitation of the driest month) were downloaded from the WorldClim database (http://www.worldclim.org/bioclim). These data are derived from monthly temperature and precipitation values recorded between 1950 and 2000 from a global network of climate stations. Elevation data were downloaded as an ASTER global digital elevation model (NASA Land Processes Distributed Active Archive Center. Aster L1B. USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota. 2001, USA). Data records for the roads and rivers of southern Sumatra were obtained from the Badan Koordinasi Survei dan Pemetaan Nasional (http://www.bakosurtanal.go.id/bakosurtanal/peta-rbi/). All layers were projected into WGS 1984 UTM Zone 48 South and clipped to the extent of the roads and rivers layer, which were the smallest datasets, including only southern Sumatra.

We extracted distance values for three of the environmental variables in ArcGIS 10 (ESRI, Redlands, California, USA). For distance to forest edge we reclassified the land cover data into forest and non-forest categories. We created a distance raster using the Euclidean distance tool that measured the distance of each pixel to forest edge. Any camera locations outside of the forest were given a distance value of zero. Distances to rivers and to roads were also extracted using the Euclidean distance tool, and new rasters were created that determined the distance of each pixel to the nearest road or river. Values for the other environmental variables were automatically extracted from the raster at each point of felid occurrence. For use in MaxEnt, all rasters were resampled to a 100-m grid cell size and a mask layer was created from the park boundaries to restrict analysis to BBSNP.

We identified 14 candidate environmental layers to include in the MaxEnt model (elevation, distance to forest edge, percent tree cover, percent mosaic tree cover/cropland, percent cropland, distance to nearest road, distance to nearest river, distance to nearest village, precipitation during the wettest month, precipitation during the driest month, annual precipitation, annual mean temperature, minimum temperature of the coldest month, maximum temperature of the warmest month). To test for correlation among variables, we conducted a Pearson's correlation matrix in Program R (R Development Core Team, 2010) and when a pair of variables had a correlation value over 0.5, we eliminated one of the pair from the dataset. We eliminated the variables that we felt were least representative of the data, and were most redundant in

Table 1
A comparison of photographic rates (no. of independent photo events per 100 trap nights) of non-*Panthera* felids from camera trap surveys in Southeast Asia.

Area	S. Sumatra[a]	N. Sumatra[b]	E. Cambodia[c]	N. Myanmar[d]	W. Thailand[e]	Lao PDR[f]
No. of trap nights	34,166	3452	18,952	10,572	12,263	469
Clouded leopard	0.15	0.41	0.02	0.45	0.05	1.07
Golden cat	0.30	0.72	<0.01	0.22	0.08	0.21
Leopard cat	0.08	0.20	0.65	0.75	1.26	2.99
Marbled cat	0.10	0.23	0.02	0.09	0.02	0.21
Jungle cat			0.11			

[a] This study.
[b] Pusparini et al. (2014).
[c] Gray et al. (2014).
[d] Zaw et al. (2014).
[e] Simcharoen et al. (2014).
[f] Coudrat and Nanthavong (2014).

the dataset. The variables that were maintained in the final dataset were: distance to forest edge, distance to nearest river, distance to nearest road, elevation, annual precipitation, and annual mean temperature.

We modeled the distributions of each of the four felid species using MaxEnt 3.3.3k (http://www.cs.princeton.edu/~schapire/maxent/). The sample input consisted of detection records for the four felid species and we allowed for duplicate detections at the same point. The environmental layers consisted of all environmental variables, as well as a spatial mask layer that restricted the analysis to BBSNP. All environmental variables were continuous. The output was in the logistic format for all analyses and the program was run with "auto features" checked (Phillips and Dudik, 2008). We used the "replicates" option, choosing cross-validation set at 50 replicates. Model performance was measured by the area under the curve (AUC) of the receiver operating characteristic (ROC) curve. The relative contribution of each variable and the permutation importance was calculated in MaxEnt as an average over the 50 replicate runs. Values were normalized to give the total percent contribution. Variable specific response curves were generated by measuring the change in logistic prediction as each environmental variable was varied while holding the others at their sample average. Standard deviation was measured using the variation in response curves across the 50 replicate model runs. This allowed us to assess how each variable affects the MaxEnt prediction of suitability. The response curves for the golden cat indicated that the model may be slightly overfitted and we considered removing the hinge and threshold features. However, Phillips and Dudik (2008) recommend that hinge features be used when the number of presence records is above 15, so we did not remove hinge or threshold features, and instead considered the possible overfitting of the model in our inference for this species.

To assess the habitat overlap between the four species we assigned 2000 random points throughout the national park. At each of these random points we extracted the value for the predicted probability of presence for each species and then used these values in a series of pairwise comparisons. We then mapped the combined predicted probability of presence in ArcGIS 10 (ESRI, Redlands, California, USA) to identify areas of high conservation priority for small felids within BBSNP.

4. Results

There were 1021 different camera locations within the park over the sampling period, and cameras were deployed for 34,166 trap nights. This resulted in 221 photographic events of our four study species; 52 of clouded leopards (0.15 photo events/100 trap nights), 104 of golden cats (0.30 photo events/100 trap nights), 30 of leopard cats (0.08 photo events/100 trap nights), and 35 (0.10 photo events/100 trap nights) of marbled cats (Table 1). In addition, we recorded 44 photographic events of tigers (0.16 photo events/100 trap nights), but none of the flat-headed cat.

The percentage of total photographic events occurring during each hour of a 24-hour day was considered a proxy to the activity patterns of the species and indicates temporal resource partitioning between the sympatric species (Fig. 2). The clouded leopard and the golden cat both exhibit a crepuscular activity pattern, with the clouded leopard also exhibiting some nocturnal activity. The marbled cat exhibited a largely diurnal activity pattern, while the leopard cat was much more nocturnal. To the degree that tigers may have influenced the activity of other felids, we note that the majority of the tiger photographs were taken during the day, suggesting a strongly diurnal activity pattern.

Species distribution models for each of the four species performed well and, despite somewhat large variances, all AUC values were greater than 0.74 (Table 2). The modeled distribution maps for all species identified areas of high predicted probability of presence within BBSNP (Fig. 3). Maps for the clouded leopard, golden cat, and marbled cat were grossly similar and showed several areas of high predicted probability of suitable conditions for the species in the north and east central portion of the park. The map for the leopard cat was fairly discrete and showed a high probability of suitable conditions in the southwestern area of the park.

The relative contribution and permutation importance of each variable was calculated for the four species as an average over the 50 replicates (Table 3). We interpreted the top three of these variables, meaning the three variables with the highest relative importance for correct prediction rate and model AUC. Annual mean temperature, distance to forest edge, and elevation were important variables to the clouded leopard model, and response curves were unimodal for each of these

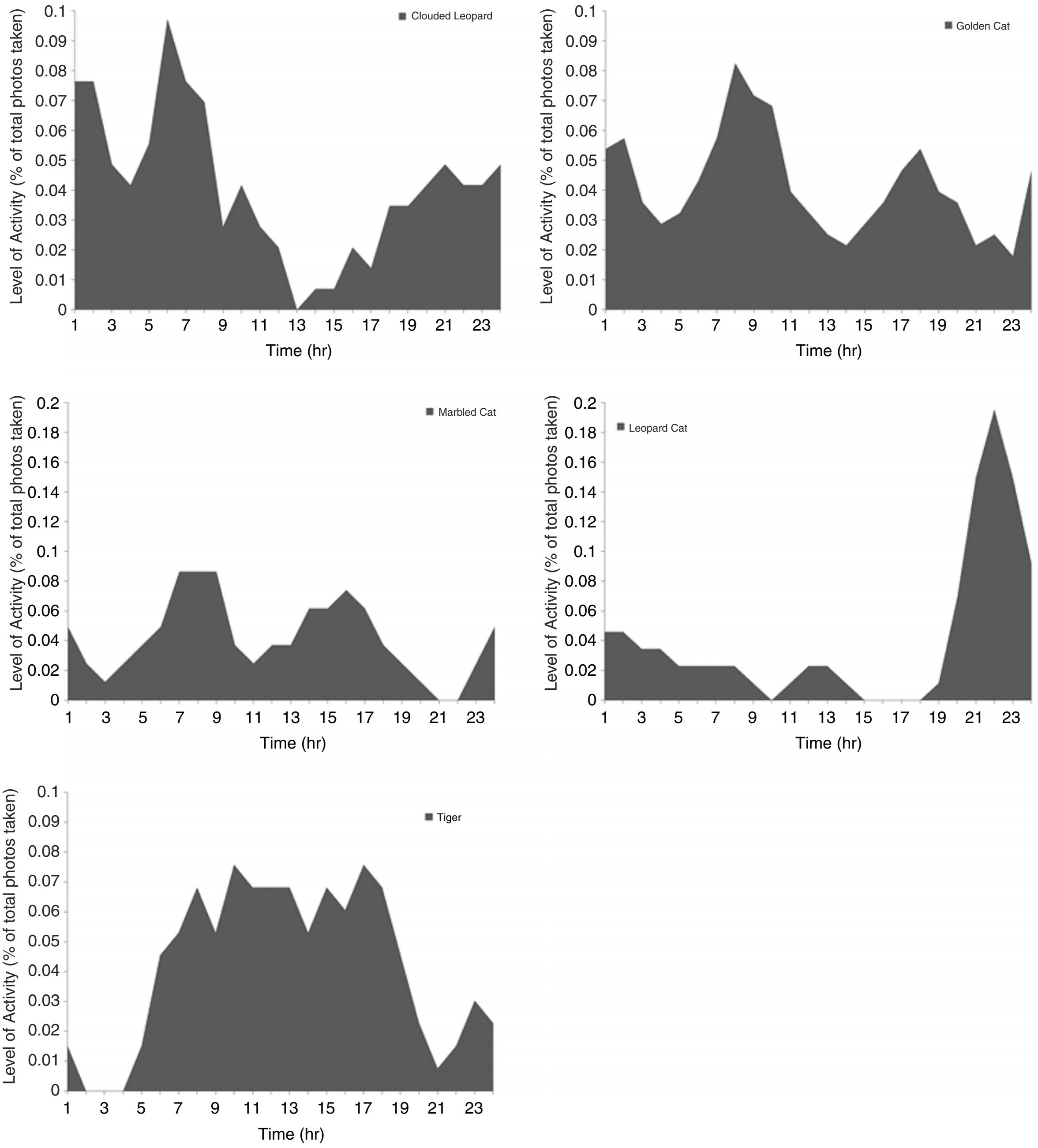

Fig. 2. The activity pattern for the four species. The number of photographs per hour based on a 24-hour day for the Sunda clouded leopard, Asiatic golden cat, marbled cat, leopard cat, and Sumatran tiger.

Table 2
The AUC value and standard deviation for each species model.

Species	AUC	Standard deviation
Sunda clouded leopard	0.757	0.227
Asiatic golden cat	0.806	0.137
Leopard cat	0.887	0.168
Marbled cat	0.740	0.280

variables. The variables of highest importance in the golden cat model were the distance to forest edge, the distance to river, and the distance to road. Response curves were roughly unimodal for these variables. Precipitation, distance to forest edge,

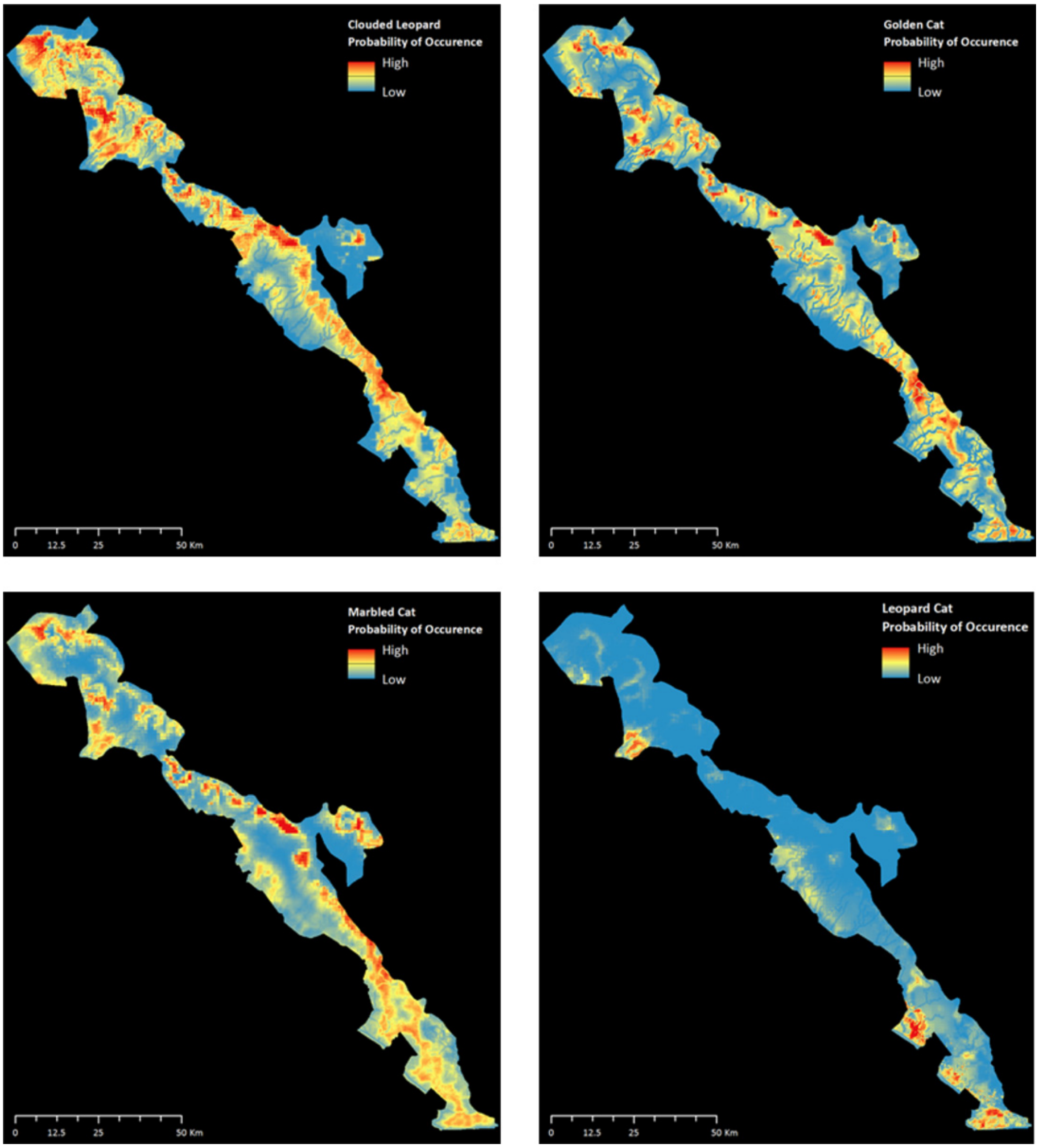

Fig. 3. Distribution maps for (a) the Sunda clouded leopard, (b) the Asiatic golden cat, (c) the marbled cat, and (d) the leopard cat. Area shown is Bukit Barisan Seletan National Park in Sumatra. Probability of presence is displayed from low (green) to high (red). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3
The relative contribution (RC) and permutation importance (PI) of each environmental variable for each species as an average over the 50 replicates. Distance to forest edge (forest distance), distance to river (river distance), annual mean temperature (temperature), distance to road (road distance), annual precipitation (precipitation), and elevation. Values are normalized to give percentages. The permutation importance was used to assess variable importance.

	Sunda clouded leopard		Asiatic golden cat		Leopard cat		Marbled cat	
	RC	PI	RC	PI	RC	PI	RC	PI
Forest distance	45.4	27.4	25.9	30.7	11	18.1	21.7	10.1
River distance	21.1	10.2	24	30.2	4.7	2.4	13.8	1.1
Temperature	11.5	34.9	18.9	11.6	6.3	1.1	21.5	27.7
Road distance	10.6	8	10.4	17.9	14.4	2	10.1	6
Precipitation	6.7	3.7	14.3	3.3	23.5	59.6	31.6	39.8
Elevation	4.8	15.7	6.4	6.3	40	16.7	1.3	15.4

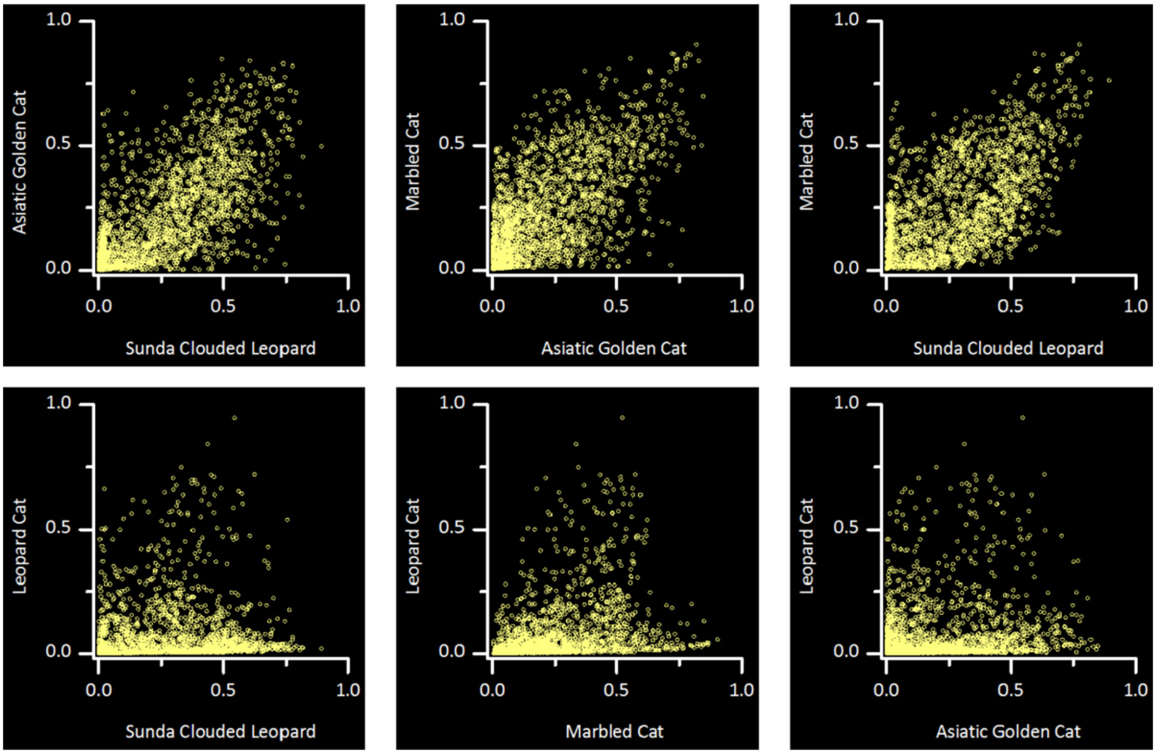

Fig. 4. Pairwise comparisons of predicted probability of presence of each species at randomly chosen points within BBSNP.

and elevation were important variables to the leopard cat model. Response curves were unimodal for precipitation and distance to forest edge, while the response curve for elevation was linear with highest predicted presence of leopard cats at low elevations and sharply declining with increased elevation. For the marbled cat, annual precipitation, annual mean temperature, and elevation were the most important variables to the final model. The response curve for precipitation was unimodal, the curve for mean annual temperature was bimodal, and the curve for elevation was logistic. It should be noted that these response curves are independent and that there may be interactions occurring in the model that are not accurately represented here.

Pairwise comparisons of each species predicted probability of presence at 2000 randomly selected locations within BBSNP show significant P-values (<0.05), implying distributional overlap for the four species (Fig. 4). However, the R^2 values for comparisons between leopard cat distribution and the distribution of the other three species are all less than 0.12. These values indicate that the leopard cat's predicted probability of presence within BBSNP is likely distinct from the other three species and that the significant P-value may be attributed to our large sample size. The R^2 values for comparisons between clouded leopards, golden cats and marbled cats are all greater than 0.38, implying some level of distributional overlap between these three species. We mapped the combined predicted probability of presence for clouded leopards, golden cats and marbled cats (Fig. 5). These data allowed for the identification of areas with a high predicted probability of presence of these three species, and indicate likely areas of high conservation importance (i.e. high felid diversity) within BBSNP.

5. Discussion

This study presents an extensive, long-term dataset of small felid distribution in Sumatra. To date, conservation initiatives for the clouded leopard, golden cat, marbled cat and leopard cat in Indonesia have been extremely limited due to a general lack of knowledge on the ecology of these species. However, high rates of habitat degradation and loss persist as a significant threat to felids in Indonesia. In large part, protected areas have become islands of habitat within a mosaic of agriculture and development, and although at a slower rate than non-protected areas, illegal logging and deforestation activities persist even within the boundaries of protected areas (Gaveau et al., 2009). Managers of Sumatra's protected areas are often hindered by a scarcity funds, a lack of trained staff, and the inability to effectively enforce regulations. They must prioritize conservation initiatives to make use of limited resources, yet often lack accurate, up to date ecological information for key species and are unable to make informed management decisions. Our data were restricted to a single national park on Sumatra. However, with the appropriate degree of caution, we feel that the systematic sampling design and the wide variety of habitat represented in our dataset allow us to use the results from this study as a base of knowledge for other areas of Sumatra and throughout the species' range.

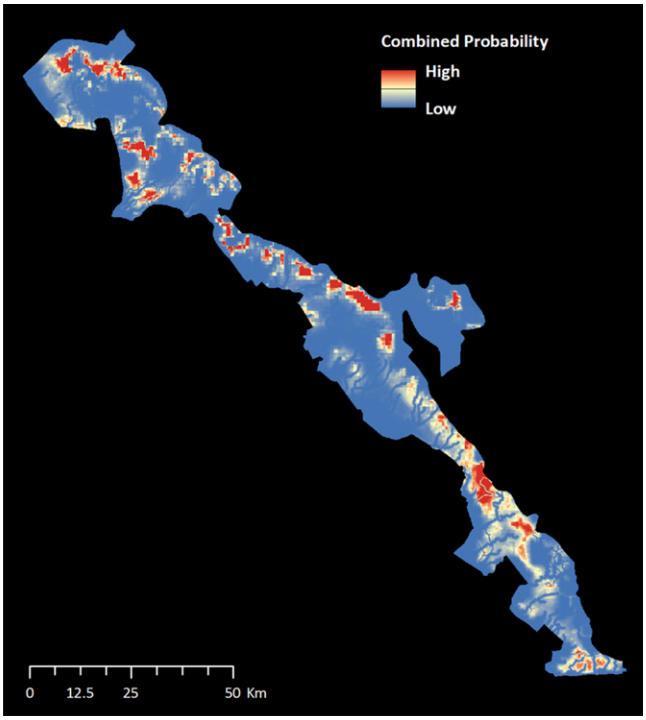

Fig. 5. Combined predicted probability of presence of clouded leopards, golden cats, and marbled cats in BBSNP. Areas in red indicate areas with a high predicted probability of presence of all three species within the park. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Although this study likely represents the largest camera trapping dataset for these four species together, our number of photographs was fairly low for the effort expended. With the exception of the leopard cat, we feel that this is likely accurately reflective of the rarity of these species. The number of photos for golden cats, clouded leopards, and marbled cats echo the speculation of their current population status in Sumatra, with the golden cat the most common, followed by the clouded leopard and then the marbled cat, thought to be the rarest of the species. Pusparini et al. (2014) recorded this same photo rate pattern in Northern Sumatra (Table 1). Somewhat surprisingly, we recorded the fewest photographs of leopard cats, the only species not classified as either threatened or endangered by the IUCN. We believe that this is likely an artifact of our sampling design and is probably not reflective of the true status of this species. Holden (2001) recorded low levels of leopard cat photos within Kerinci Seblat National Park, as did Pusparini et al. (2014) in Gunung Leuser National Park. In addition, Mohamed et al. (2013) reported that the density of leopard cats was higher in disturbed forests than sustainably managed forests. Finally, leopard cats are known to inhabit agricultural landscapes (Scott et al., 2004; Rajaratnam et al., 2007) and although our camera blocks were designed to sample the full gradient from forest edge to interior, we did not have any sites outside of the national park and may have missed sampling integral habitat for this species. However, it is important to note that several mainland studies that occurred inside of national parks reported the leopard cat as the most common species (Gray et al., 2014; Zaw et al., 2014; Simcharoen et al., 2014; Coudrat and Nanthavong, 2014). In addition, we have also documented high levels of human–leopard cat conflict at the edge of the park (McCarthy, 2013), and the species is commonly found in local wildlife markets (Pusparini et al., 2014), so we cannot ensure that our lack of photographs is due solely to our camera placement. Instead, these data imply the necessity of further research before asserting that the species is common in Sumatra.

We did not record any photographs of the flat-headed cat during the duration of the study. This is not unexpected, as Wilting et al. (2012) does not predict a high probability of occurrence for the flat-headed cat in BBSNP, and it has not been previously reported in the park. We did not specifically target habitats where the species is thought to occur more commonly (i.e. riparian areas). However, the randomized design of our study did include camera trapping in some of these areas and so the lack of photographs indicate the likelihood of its absence from BBSNP.

While we cannot directly compare the photo rates of species across studies, an examination of relative abundances among other studies in Southeast Asia is useful. We see some difference of relative abundances among the various studies, with the leopard cat the most commonly photographed species in the mainland studies, and some slight variations among the other three species. However, the photo rates in all of the studies remain fairly low (Table 1). In fact, from our study, the photo rates of all four small felid species were low even when compared to the photo rate obtained for the endangered Sumatran tiger. We recognize that photo rates are not comparable across species, but suggest that the very low photo rates for our study species imply that none of the four species can be considered common in BBSNP, and highlight the urgency of conservation initiatives for small-felid species in Sumatra. These results also indicate that a more detailed and comprehensive evaluation of the overall population of these species is called for in order to ensure that their range-wide status and extinction risk is accurately reflected.

Identification of areas with a high probability of presence provides an important tool for managers. The distribution maps generated by the model show predicted areas of high and low probability of presence for each species. Although there is definite distinction among the distributions, there is some degree of gross sympatry among the clouded leopard, the marbled cat and the golden cat, and we can identify several areas within BBSNP that have a high combined predicted probability of presence for these three species. The large-scale data generated from the distributional maps are very useful to park managers. They may act as a rough tool to help identify areas of conservation priority and subsequently direct ranger patrols, anti-poaching efforts, and anti-encroachment operations.

In addition to being an important tool for managers, our species distribution maps also allow us to make inferences about the ecology and conservation of the four species in Sumatra. When carnivores occur sympatrically there is often evidence of increased habitat specificity and either spatial or temporal resource partitioning, allowing the occurrence of multiple sympatric species Johnson et al. (1996). Our data indicate a level of gross spatial overlap between the clouded leopard, the golden cat, and the marbled cat. They all appear to be relatively intolerant of anthropogenic features, all occurring most commonly at moderate distances from roads and forest edges. However, the species are also exhibiting some level of fine-scale spatial niche partitioning. The clouded leopard appears to inhabit areas a moderate distance from rivers, and at a moderate elevation. The golden cat also inhabits areas a moderate distance from rivers, although at a slightly lower elevation. The marbled cat occurs slightly closer to the forest edge and a moderate distance from rivers. The leopard cat's habitat use is the most spatially discrete, utilizing habitat very close to the forest edge and at low elevations. Because of its presence at the forest edge, it also occurs much closer to roads than the other species which are more interior. The forest edge and lower elevation also means that the leopard cat experiences slightly higher temperatures than the other species. These predicted distributions are roughly consistent with the findings of Pusparini et al. (2014) who documented clouded leopards and marbled cats most commonly recorded by camera traps in medium elevation hills, and leopard cats most commonly recorded in lowland areas.

In addition to varying spatial distributions, it appears that the species are further partitioning resources with discrete activity patterns. The clouded leopard and the golden cat are both crepuscular. This differs from the results of Hearn et al. (2013) on Borneo, who found the clouded leopard to be nocturnal, but concurs with other studies on Sumatra (Ridout and Linkie, 2009; Pusparini et al., 2014) and on Borneo (Cheyne and MacDonald, 2011). Although the activity peaks of the clouded leopard and golden cat are slightly offset from each other, there is a fair amount of overlap. We believe that this amount of overlap between two similar-sized species can be explained by a difference in the exploitation of resources. Although relatively little is known about the ecology of wild clouded leopards, morphology and anecdotal reports indicate that they are fairly arboreal and able to prey on species in the canopy (Nowell and Jackson, 1996; J.L. McCarthy, Pers. Comm.). By preying on species in the canopy, the clouded leopard is able to exploit resources unavailable to the more terrestrial golden cat, and there is probably little competition between the species despite temporal overlap. The marbled cat occurs fairly sympatrically with the clouded leopard and golden cat, but is temporally separated by a diurnal activity pattern. This is contrary to previous reports of the species that imply that the rarity of sightings may be explained by a nocturnal activity pattern (Nowell and Jackson, 1996), and confirmed by recent sightings and anecdotal reports (J.L. McCarthy, Pers. Comm; Grassman and Tewes, 2002; Morino, 2009). The leopard cat appears to be largely nocturnal, with little activity recorded during the day. Since it experiences a relatively low amount of spatial overlap with the other species, this most likely reflects its prey preference for small murids which are also active at night, rather than a niche partitioning between it and the other three species. As they appear to occupy areas of greater human presence, the leopard cat's nocturnal nature may also reflect a mechanism to avoid human activity.

Although the Sumatran tiger was not one of our study species, there has been speculation as to their effect on the habitat use and activity of smaller felids, particularly the clouded leopard. Our data was basic, yet indicates some evidence of temporal separation between tigers and the smaller species, particularly the clouded leopard and golden cat. Tigers in BBSNP exhibited a strongly diurnal activity pattern, with the majority of photographs taken between 06:00 and 19:00, while both the clouded leopard and golden cat were more crepuscular or nocturnal. Our study was not focused on this issue and we were unable to address anything beyond the activity pattern of the five species. However, these data do suggest that there may be some avoidance of tigers by the smaller species. It is unknown whether they are avoiding areas of high tiger density for some reason, or whether they are still present but altering their habitat use. More detailed studies that assess spatial and movement data are called for, especially in light of frequent relocations of "problem tigers" in Sumatra (Priatna et al., 2012).

With insight into the ecology of Sumatran clouded leopards, golden cats, leopard cats, and marbled cats, we are able to begin to further elucidate threats that they may face and to direct conservation measures. Currently, the leopard cat is considered a species of least concern in Southeast Asia and Sumatra; however, our data may indicate that careful consideration of its status in Sumatra is called for. The leopard cat is utilizing habitat at the very edge of the forest and therefore is at greater risk of conflict with humans, and experiences a higher likelihood of habitat disturbance. Previous research indicates that the leopard cat may adjust well to human presence, using the forest as a refuge and exploiting agricultural landscapes for prey. We do not dispute this assertion, but the low number of photographs that we recorded, even at the forest edge, implies that the species is not occurring in high numbers inside of the national park, and thus is not benefiting from the protection provided by the park. We did not conduct camera trapping outside of the national park, and the species may be occurring in large numbers in agricultural landscapes. However, if it is not utilizing the park for protection, it may be more vulnerable than previously thought. This is confirmed by reports of high levels of leopard cat–human conflict around BBSNP and indications of retribution killing of the species (McCarthy, 2013). The clouded leopard, golden cat and marbled cat all have more interior distributions than the leopard cat; however, they are still utilizing habitat only a moderate distance from the forest edge. This highlights the importance of protection within the park, as the areas that the species inhabit are fairly accessible to humans and thus vulnerable to overexploitation of both cats as well as other components of their habitat, i.e. prey and vegetative cover. The rarity of marbled cats and clouded leopards in particular is also emphasized by this study. Despite large-scale, long-term sampling, the number of photographs of these species in BBSNP was relatively low. Previous accounts have attributed low numbers of sightings of these species to an arboreal or nocturnal nature (Nowell and Jackson, 1996). Our cameras were fully functional throughout a 24-hour time period and the data indicate that neither species is nocturnal, so that cannot explain the low number of sightings. The arboreal nature of the species may limit the number of photographs, but we believe that this cannot be assumed, and instead suggest that conservation initiatives for the species be implemented on the basis of the current data which suggests that both species occur at low numbers and should be considered for increased protection.

This study not only contributes important ecological information for the four species, but also demonstrates an easily replicable method of examining small felid distribution in Southeast Asia. The information is essential to the implementation of conservation initiatives for the species and important for the effective management of protected areas. To date, there has been little support for targeted studies of small felids in Southeast Asia, and thus it is often difficult to execute a large-scale, long-term study specifically on small cats. Yet, there have been a plethora of camera trap studies focused on tigers, and photographs of small cat species are consistently recorded as a byproduct during these efforts. For the researcher, the low number of photographs makes traditional analysis difficult, and many do not even report the data. However, this study provides a research and analysis outline that is easily adjusted for use throughout the species range and in a standard format. Collaboration and examination of data on clouded leopards, golden cats, marbled cats, and leopard cats across their range is essential to effectively and efficiently conserve these species within a rapidly changing landscape.

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