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Cat coexistence in central Sumatra: ecological characteristics, spatial and temporal overlap, and implications for management

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Abstract

At least six species of wild cats live in Sumatra. Many are globally threatened and yet their ecology is poorly understood. We investigated ecological characteristics and spatial and temporal overlap among cats in central Sumatra using data from systematic and opportunistic camera trapping in five major forest blocks. We developed occupancy models assessing probability of site use by each cat based on (1) photo-trap rates of other species at the same locations and (2) landscape-level factors extracted from geographic information systems. We also used two-species co-occurrence models to assess spatial overlap and used kernel density estimates on circular data to assess temporal overlap between species pairs. We photographed five cat species: Sumatran tigers, Sunda clouded leopards, Asiatic golden cats, marbled cats and leopard cats. Four cats were present in all sampling blocks and one sampling block had all five cats. Spatially, cat distributions varied among forest types, within the sampling blocks and across elevation. We placed camera traps at elevations ranging from 6 to 460 m above sea level. The five cats used statistically different elevations, with golden cats found at highest elevation. Site use by tigers and leopard cats negatively covaried with distance to protected areas. Clouded leopard presence covaried positively with altitude. Leopard cat presence covaried with the photo-trap rate of tigers, whereas the presence of tigers covaried with the photo-trap rate of non-cat carnivores. We found little evidence of spatial avoidance among cats at camera sites. Temporally, species more similar in size, or with similar-sized prey, had lower overlap, suggesting temporal avoidance. We identified six mechanisms promoting coexistence of central Sumatra cats. Knowledge of interspecific interactions may improve the effectiveness of management aimed at conserving the increasingly threatened wild cat community.

Introduction

Sumatra maintains rich mammalian diversity including many carnivores, especially wild cats. At least six of nine living wild cats known to be distributed in Indonesia have been recorded in Sumatra (Nowell & Jackson, 1996). For comparison, the neighboring island of Borneo, which is larger in size, has only five; while Java, after losing the Javan tiger, has only three species remaining. There are no wild cats recorded east beyond the islands of Borneo or Bali.

Except for the Sumatran tiger *Panthera tigris sumatrae*, there is little information on natural history or ecological characteristics of most other smaller cats in Sumatra. Until recently, information on Sumatran small cats was limited to species lists in management plans for certain protected areas (e.g. Ministry of Forestry, 2006), databases pertinent to areas of interest such as endemic bird areas (e.g. Holmes & Rombang, 2001) or, less commonly, reports after sightings or field investigations (e.g. Bezuijen, 2000; Wibisono & McCarthy, 2010). We lack basic knowledge regarding whether the fishing cat *Prionailurus viverrinus* occurs in Sumatra (Melisch *et al.*, 1996; Duckworth *et al.*, 2009). Although there have been introductory studies on the distribution and abundance of the Sunda clouded leopard *Neofelis diardi* (Santiapillai & Ashby, 1988; Santiapillai, 1989; Hutajulu *et al.*, 2007), only recently have new studies on other small cats emerged from Sumatra and elsewhere, mainly resulting from by-catch data from camera trapping studies. These include a study on occupancy of Sunda clouded leopard *N. diardi* and Asiatic golden cat *Catopuma temminckii* (Haidir *et al*., 2013), a community study on small- and medium-sized cats in Northern Sumatra (Pusparini *et al*., 2014), and a study on density of clouded leopards from Kerinci Seblat (Sollmann *et al*., 2014). An example from outside Sumatra is a recent study on guild and habitat association of clouded leopards, leopards and tigers from Thailand (Ngoprasert *et al*., 2012). As high rates of forest loss and habitat degradation have been documented in Sumatra (Uryu *et al*., 2010), and many cats on the island are threatened in addition to the critically endangered Sumatran tiger (Nowell & Jackson, 1996; IUCN, 2001), obtaining ecological information on Sumatran wild cats is an urgent need if they are to be conserved in Sumatra.

As a by-product of active tiger research in central Sumatra (Sunarto *et al*., 2012, 2013), information on other wild cats is available through tiger camera trapping studies. We used this information to investigate natural history, ecological characteristics and potential for species interactions of the Sumatran cat community, which appears to consist of competing sympatric species. Understanding the role of interspecific competition and resource partitioning may enhance effective management of this cat guild. In this study we address knowledge gaps by determining (1) general ecological characteristics of each cat species in relation to geographic location and site conditions; (2) factors affecting probability of site use by each cat species; (3) the extent of interactions between cat species pairs as indicated by spatial and temporal co-occurrence. Finally, we discuss management implications.

Study area

This study occurred in the southern Riau landscape (~30 000 km^2), central Sumatra (Fig. 1) within the Kampar-Batanghari region (Whitten *et al*., 2000), which includes four major protected areas: Rimbang Baling Wildlife Reserve, Tesso Nilo National Park, Bukit Tigapuluh National Park and Kerumutan Wildlife Reserve. Types of natural forest include peat swamp in the Kerumutan and Kampar Peninsula, dry and relatively flat lowland forest in Tesso Nilo, transition between the flat and hilly forests in Peranap and hilly forest in Rimbang Baling. Precipitation ranges from 2000 to 3000 mm annually, and humidity is high (>80%). Our study area is generally categorized as lowland (<500 m) with elevation across camera stations ranging from 6 to 460 m. A more detailed account of the area is available in Sunarto *et al*. (2012, 2013).

Materials and methods

Photographic sampling with camera traps

Camera trapping originally focused on Sumatran tigers but also yielded images of other wildlife species (Sunarto *et al*., 2013). Five systematic sampling blocks (~160 km^2 each) were selected from the major forest blocks in approximate proportion to their occurrence in the landscape (Fig. 1). Within each block, we overlaid a 2 × 2 km grid and placed camera stations in every other grid cell with a minimum of 20 stations per block, with two DeerCam® 200/300 (Non Typical, Inc., 860 Park Lane, Park Falls, WI) cameras per station, active 24 h, for 3 months. This cell size was originally chosen based on its practicality for field navigation, and analysis related to home-range use of tigers to ensure 'non-zero probability of being photographed' under capture-mark-recapture assumptions. We also used opportunistic camera placement for 1–3 months in additional areas across the landscape (Sunarto *et al*., 2013). No

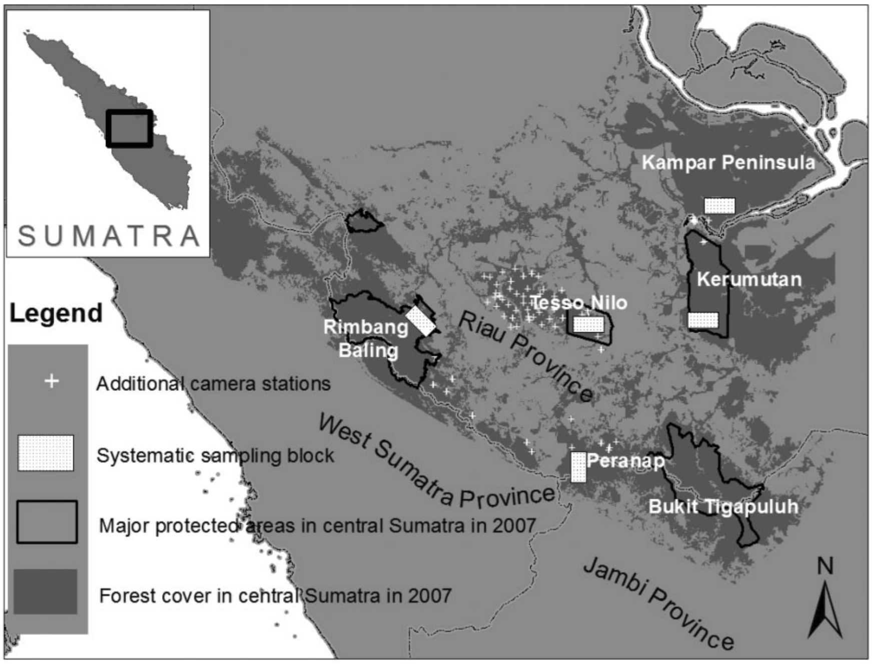

Figure 1 Map of study area showing existing forests, major protected areas and position of camera trap sampling blocks in Riau Province, central Sumatra.

Table 1 Characteristics of five sampling blocks in central Sumatra and levels of systematic sampling effort conducted from 2005 to 2007

	Kampar	Kerumutan	Tesso Nilo	Peranap	Rimbang Baling
Major soil type	Peat	Peat	Mineral	Mineral	Mineral
Composite criteria[a]	Alluvial and swamp	Alluvial and swamp	Sedimentary	Sedimentary	Metamorphic
Protection status	No protection	Wildlife reserve	National park	No protection	Wildlife reserve
Ex-logging concession	Yes	No	Yes	Yes	Partly
Observed logging impact	High	Low	Very high	Medium	Low
Terrain	Flat	Flat	Generally flat	Flat to gentle hill	Gentle to steep hill
Wetness	Mostly inundated	Mostly inundated	Mostly dry	Dry	Dry
Total size of core forest block (in 1000 ha)[b]	306	379	86	186	168
Sampling period	20 July 2007–03 November 2007	7 September 2006–17 December 2006	31 May 2005–11 September 2005	16 September 2005–29 December 2005	19 April 2006–28 July 2006
# Trap stations[c]	18	22	22	22	20
Effective trap nights	1132	1868	1618	1321	1574
Camera loss	16	0	3	3	0
Human pictures	28	1	85	17[d]	11

[a] Combination of geological, bioclimatic, geomorphological and topographical maps as identified by Laumonier (1997).

[b] Obtained by measuring the forest area based on interpretation of Landsat images acquired in 2007 (carried out by WWF Indonesia GIS Team) after reducing with 3 km buffer, assuming edge effect.

[c] Counted based on the position in 2 × 2 km grids. For the very rare case of cameras being moved during sampling period due to security or other reasons, they are considered as one trap station if location is still in the same 2 × 2 grid. Total loss/failure of cameras in a given grid during sampling period render the trap station being uncounted.

[d] Includes the presence of forest dwelling indigenous people who live on subsistence hunting.

baits or lures were used. We placed cameras non-randomly in each predetermined grid cell to optimize tiger captures (e.g. in suitable habitat with tiger sign, in likely tiger travel paths on roads and trails) while avoiding human disturbance/vandalism. At each selected site, the team installed a pair of opposing cameras (during systematic samplings) or a single camera (in *ad hoc* samplings) at knee height, preferably on a living tree, at ~2–3 m from the center of the trail where animals were likely to pass. Although the study did focus on maximizing tiger detections, placement of cameras at a knee height also targeted tiger cubs, potential prey animals and other small carnivores. We do note however that camera spacing and placement was tiger centric, thus may limit inference regarding small cat habitat preferences. Nonetheless, we accumulated 7513 trap nights from systematic surveys at 104 locations (Table 1) and 5315 additional trap nights from opportunistic surveys at 65 locations. We combined all stations for habitat modeling, but to compare trap rates of cats, prey animals and other carnivores among sites, we only used data from systematic samplings as each site had similar effort.

Species trapping rates and landscape variables

For each sampling block, we calculated activity level or trap rate of cats, other carnivores, potential prey and humans to use as predictor variables in modeling occupancy of each of five species. Trap rate was calculated by dividing the number of independent photos (i.e. photographic events of distinct animals within 30-min time intervals regardless of the number of photographs) by sampling effort (per 100 trap nights) as in previous studies (Kelly, 2003; O'Brien, Kinnaird & Wibisono, 2003). We extracted habitat variables from a 500-m radius surrounding each camera station from a geographic information system (GIS) similar to other studies (Kelly & Holub, 2008; Davis, Kelly & Stauffer, 2011). These variables included forest area, % tree cover and % shrub cover. We also calculated distance to major public road, distance to core forest area, distance to forest edge, distance to core of protected areas, distance to fresh water, precipitation and altitude. Original sources and further details of GIS data are presented in Supporting Information Appendix S1.

Modeling habitat use

We built single-season occupancy models (MacKenzie *et al.*, 2006) in Program PRESENCE (Hines, 2006) to determine factors impacting site use for each species. Detection histories were based on detection and non-detection data from camera traps. Site covariates consisted of photo-trap rates of each cat species, other carnivores, and three categories of prey and humans. Similar to Davis *et al.* (2011) we categorized potential prey based on their average body mass from the literature, into large (>20 kg), medium size (5–20 kg) and small (<5 kg). We also used GIS variables described earlier as additional site covariates.

We developed models by first entering each covariate in a univariate model. Covariates that improved model fit compared with the constant model (without covariate) were then combined to develop models with multiple variables. Models were evaluated based on Akaike information criteria (AIC) (Burnham & Anderson, 1998).

Species interaction

Spatial and temporal co-occurrence

We investigated spatial overlap using two-species co-occurrence models for each pair-wise combination of cats with adequate detection data. We examined three possible scenarios following MacKenzie *et al.* (2006): (1) site occupancy of one species is influenced by presence of the other; (2) species detections are independent from each other; (3) detection of a species depends on the presence of another species. We hypothesized that cats most similar in body mass would avoid each other. However, we anticipated exceptions for similar-sized species that had either distinct morphological characters or those that had different physical capabilities (e.g. arboreal vs. terrestrial).

We considered two species to occur together less often than random (potential avoidance), when φ, the species interaction factor (SIF), was <1, and to occur together more often than random when $\varphi > 1$. Two species were considered spatially independent if $\varphi = 1$ or the standard errors overlapped 1.0. Following MacKenzie *et al.* (2006) we developed two models (one with φ estimated and one with φ set = 1) and formally compared fit based on AIC values. We considered models competing if $\Delta\text{AIC} < 2$ (Burnham & Anderson, 1998). Detection history at each camera site consisted of three to five sampling occasions with each occasion representing a 1-month sampling period involving one or more cameras within the same 2 × 2-km grid cell.

We investigated temporal co-occurrence between cat pairs based on their daily activity patterns. We pooled data across all sites, including those from systematic and opportunistic sampling. We used kernel density estimation (KDE) on circular data following Ridout & Linkie (2009) to characterize activity patterns for each species and calculated the coefficient of overlap (Δ) between pairs using their equation 3.1 with a smoothing parameter (c) of 1.0.

Mechanisms for coexistence

Based on our findings and the literature, we identified and ranked the likely mechanisms used by Sumatran cat pairs to maintain coexistence. When differences in characteristics such as prey size were extreme, we considered the mechanism to be 'most probable'. When differences were slight, the mechanism was considered 'unlikely'.

Results

Status and characteristics of wild cats based on literature

The cat species recorded in Sumatra vary in morphological characteristics, physical abilities and in geographic range, distribution and habitat (Supporting Information Appendix S2). Average body mass spans more than an order of magnitude from the marbled cat (4 kg) to the tiger (185.5 kg) (Fig. 2). Different cats focus on different prey types ranging from aquatic animals for flat-headed and fishing cats to large ungulates for tigers. Although most Sumatran cats dwell in natural forests, some can live in relatively disturbed habitats including secondary forests and plantations. Flat-headed cats, fishing cats and leopard cats are known to be good swimmers, and the first two are recognized as well-adapted to wetlands. Clouded leopards and marbled cats are excellent tree climbers exhibiting partly arboreal lifestyles. Two species of cats (the leopard cat and fishing cat) are either primarily or totally nocturnal, one (flat-headed cat) is unknown and the remaining four can be active at day and night.

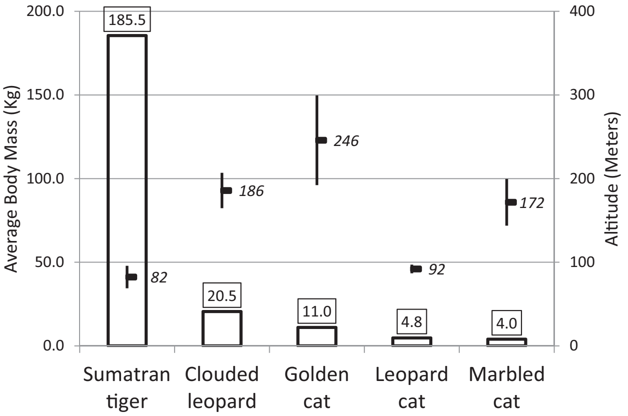

Figure 2 Known average body mass (bars and boxes) and altitudinal distribution (dots) of cat photo-captures in the landscape. Altitudinal values indicate mean ± standard error of elevation (in meters) of all camera traps where respective species was captured.

Wild cats, potential prey and other carnivores: comparison among sites

We photo-trapped five species of wild cats. Two cats, clouded leopards and leopard cats, were present and widespread in all sampling blocks (Fig. 3). Two cat species, flat-headed cats and fishing cats, might be present in the area, but we did not detect them in this study.

Rimbang Baling, the hilly forest site, was the only sampling block where all five cat species were photographed. In Peranap, we photographed all smaller cats but no tigers. We photographed four cat species in Kerumutan and Tesso Nilo, and in Kampar, we only photographed two cat species (Fig. 3).

Golden cats generally inhabited the highest elevation (mean = 245.8 m) and were the most restricted in distribution, found only in two, relatively higher elevation blocks: Peranap and Rimbang Baling (Figs 2 and 3). Clouded leopards and marbled cats generally occurred in the middle range (150–200 m) of elevation in the study area, while the two species of extreme sizes, tigers and leopard cats, generally occurred at lowest elevations, below 100 m.

For large prey, photographic rates were highest for barking deer *Muntiacus muntjak* and wild boar *Sus scrofa*;

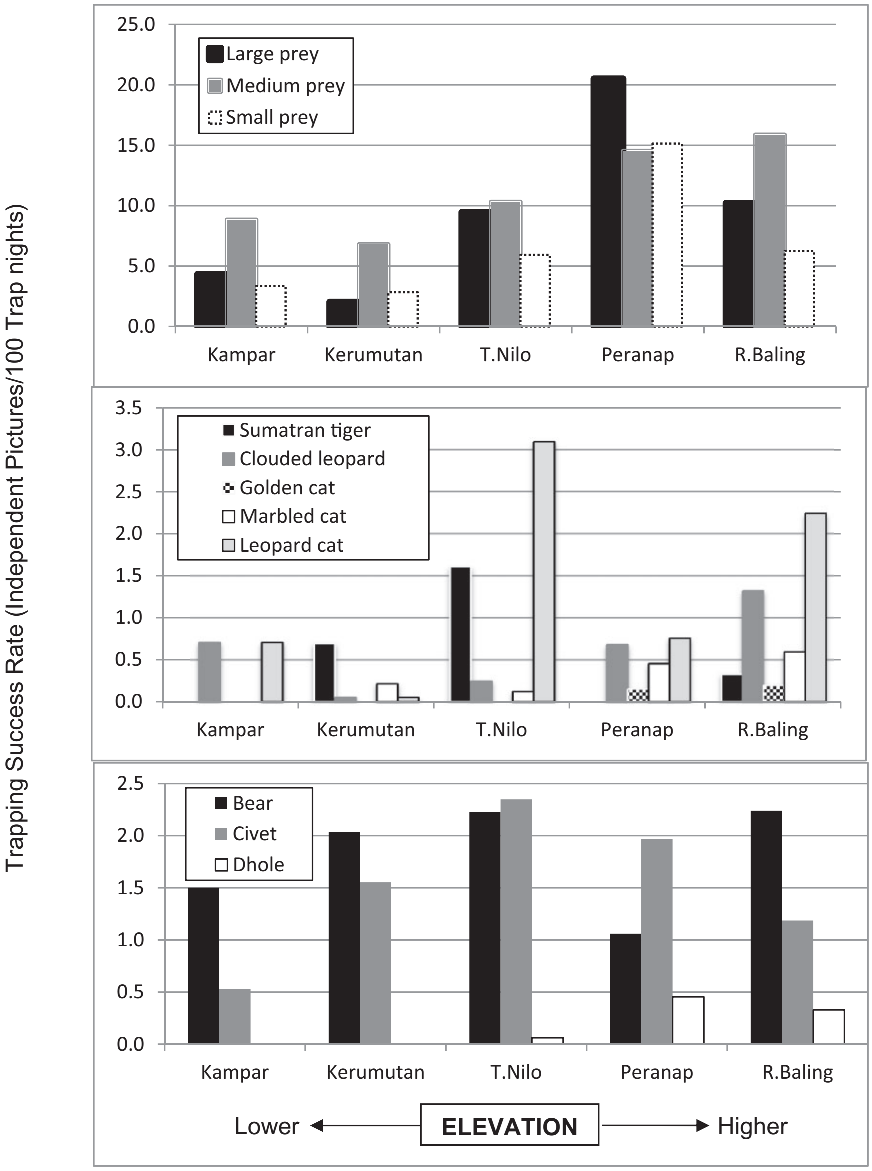

Figure 3 Trapping success rate for five cat species, potential prey and other major carnivores in five forest blocks sampled.

for medium-sized prey were highest for pig-tailed macaques *Macaca nemestrina* and common porcupines *Hystrix brachyura*; and for small prey were highest for mousedeer (*Tragulus* spp.) and Malay civets *Viverra tangalunga* (Supporting Information Appendix S3). Peranap had the highest trapping rates of potential prey of almost all sizes (Fig. 3) followed by Rimbang Baling, Tesso Nilo, Kampar and Kerumutan.

Three mammalian carnivore species/groups seemed likely to compete with cats for prey: sun bears *Helarctos malayanus*, civets (Malay civet *V. tangalunga* and others from Family Viverridae) and dholes *Cuon alpinus*. Sun bears were relatively commonly recorded in every area but had the lowest trap rates in Peranap (Fig. 3). Civet trap rates peaked in the flat lowlands of Tesso Nilo while dholes, which were not recorded in peatland forests, had the highest trap rate in Peranap.

Habitat use models

Probability of site use by leopard cats significantly and positively covaried with trap rates of Sumatran tigers, while site use by tigers significantly and positively covaried with trap rate of non-cat carnivores. Based on the best model, no other species' trap rate significantly covaried with the probability of site use by any cat (Table 2).

Out of 10 landscape GIS-extracted variables used in occupancy models, only three were statistically important factors determining cat species-specific probability of habitat use. These include distance to protected area (negatively associated with probability of habitat use by tigers and leopard cats), distance to public roads (negatively associated with probability of habitat use by tigers) and altitude (positively

Table 2 Results from occupancy modeling showing the effects of trapping rates of other species on the probability of sites use by five cat species

	Sumatran tiger		Clouded leopard		Golden cat		Leopard cat		Marbled cat	
Parameter	Best model	Model average	Best model	Model average	Best model	Model average	Best model	Model average	Best model	Model average
Intercept	**–1.38 (0.22)**	–1.38	**0.97 (0.37)**	–0.94	**–2.28 (1.10)**	–2.38	0.03 (0.41)	–0.02	–1.25 (0.91)	–0.95
Sumatran tigers	NA	NA	–	0.00	–	–0.01	**2.27 (1.04)**	2.28	NA	0.00
Clouded leopard	NA	NA	–	NA	1.68 (1.55)	0.85	NA	NA	NA	0.00
Golden cat	NA	NA	0.42 (0.38)	0.27	–	NA	NA	NA	NA	NA
Leopard cat	NA	NA	–	NA	–	NA	NA	NA	NA	0.00
Marbled cat	NA	NA	–	NA	–	NA	NA	NA	NA	NA
Malayan sun bear	NA	NA	–	0.00	–	0.00	NA	NA	NA	0.67
Dhole	NA	NA	0.70 (0.64)	0.56	–	0.00	NA	NA	NA	NA
Non-cat carnivores	**0.65 (0.19)**	0.62	–	0.00	–	0.00	0.44 (0.24)	0.32	NA	0.55
Large prey	NA	0.00	–	0.04	–	0.10	NA	NA	NA	0.01
Medium prey	NA	0.00	–	0.00	0.68 (0.36)	0.49	NA	NA	1.99 (1.24)	1.05
Small prey	NA	0.00	–	0.00	–	0.00	NA	0.03	NA	0.00
Humans	NA	0.12	–	0.00	–	0.00	NA	NA	NA	0.00

Numbers show untransformed estimates of coefficients for covariates (betas) and standard error in parentheses; values of covariates were normalized before being entered in the model. **Bold** indicates values that do not overlap zero implying significant effect.
NA, not applicable.

Table 3 Effects of GIS-extracted landscape variables on the use of habitat by five cat species

	Sumatran tiger		Clouded leopard		Golden cat		Leopard cat		Marbled cat	
Parameter	Best model	Model average	Best model	Model average	Best model	Model average	Best model	Model average	Best model	Model average
Intercept	**–3.56 (0.71)**	–3.36	–0.51 (0.35)	–0.49	–11.72 (16.83)	–6.09	–1.11 (0.57)	–1.13	1.19 (1.75)	0.39
Distance to forest edge (m)	NA	–0.11	NA	–0.27	NA	0.02	NA	0.00	NA	0.02
Distance to core of protected area (m)	**–1.57 (0.45)**	–1.53	NA	NA	NA	–0.02	**–1.35 (0.43)**	–1.34	NA	0.00
Distance to core of large forest block (m)	NA	NA	NA	NA	NA	–0.03	NA	0.00	NA	–0.01
Distance to major public road (m)	**–2.96 (1.11)**	–2.74	NA	NA	NA	–0.03	NA	0.01	NA	0.00
Distance to water (m)	NA	0.07	NA	NA	NA	NA	NA	–0.05	NA	0.00
Precipitation (mm)	NA	NA	NA	–0.46	NA	NA	NA	0.00	–5.69 (4.36)	–2.40
Altitude (m)	NA	NA	**2.97 (1.01)**	3.51	NA	NA	NA	0.00	11.78 (7.02)	6.42
Forest area (ha)	NA	NA	NA	NA	16.57 (27.11)	0.06	NA	0.00	NA	0.08
Tree cover (%)	NA	–0.15	NA	NA	NA	7.01	NA	–0.01	NA	0.00
Shrubs/herbaceous plant cover (%)	NA	0.05	–	NA	–	–	0.90 (0.47)	0.85	–	–0.01

Numbers show untransformed estimates of coefficients for covariates (betas) and standard error in parentheses; values of covariates were all normalized before being entered in the model. **Bold** indicates values that do not overlap zero implying significant effect.
GIS, geographic information system; NA, not applicable.

associated with probability of habitat use by clouded leopards) (Table 3).

Spatial and temporal co-occurrence

In all cases, the estimated SIF was always greater than 1.0 (Fig. 4), indicating spatial co-occurrence rather than potential avoidance. However, none of these models out-competed the model where cats occurred independently (SIF = 1) and most had 95% confidence intervals that included 1. Based on the delta AIC between models that estimated the SIF and those with SIF held constant at 1.0 (independence), we found statistical support for only one model that estimated SIF for the golden cat and marbled cat (all other $\Delta\text{AIC} > 5$; Fig. 4). However, this model had difficulty converging perhaps due to limited sample size.

Based on KDE estimates of temporal activity, we found that, except between clouded leopards and marbled cats [Δ (SE) = 0.50 (0.08)], the lowest coefficients of overlap were found between species that were most similar in body mass,

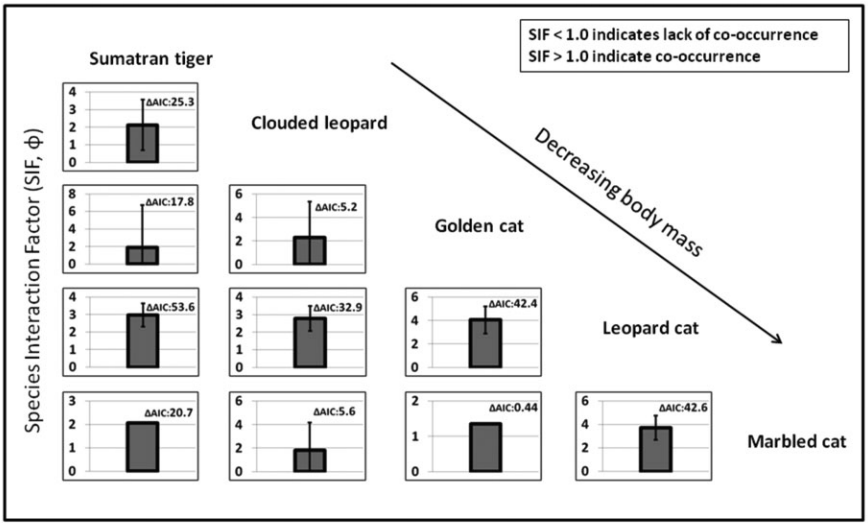

Figure 4 Species interaction factor (SIF, φ) and confidence intervals between pairs of cat species based on their spatial co-occurrence across the camera trap stations. Delta Akaike Information Criterion (AIC) presented is based on comparison of the models that estimate SIF to the model that holds SIF constant, $\varphi = 1$. We present only the model that estimated SIF and note that none were the top model and only one was a competing model based on the delta AIC. Those without confidence intervals displayed had low sample sizes and thus difficulty converging.

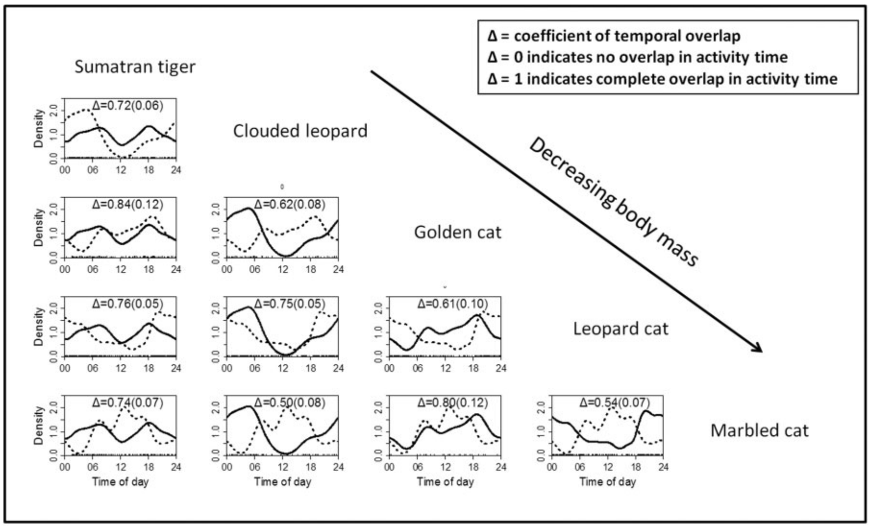

Figure 5 Overlap of activity patterns between cat species pairs based on kernel density estimate on circular data. Solid lines represent species in each column; dotted lines represent species in the row. Numbers indicate coefficient of overlap, Δ (standard error).

and in fact many had nearly opposite activity patterns. Tigers had the lowest overlap with the next largest cat, clouded leopards [Δ (SE) = 0.72 (0.06)]. Golden cats had lowest overlap with the next smaller cat, leopard cats [Δ (SE) = 0.61 (0.10)], or the next larger cat, clouded leopards [Δ (SE) = 0.62 (0.08)] (Fig. 5).

Mechanisms for coexistence

Based on differences in morphological and ecological characteristics and patterns of spatial and temporal co-occurrence, we identified six possible mechanisms by which cats maintain coexistence (geographic separation, elevational segregation, use of vertical habitat strata, other microhabitat features, temporal segregation and prey size) and rank their plausibility in Table 4.

Discussion

This study provides plausible mechanism regarding factors permitting co-occurrence among wild cats in central Sumatra, which may be used to support on-the-ground conservation and management of the cat community.

Based on the literature, cat morphology influences prey preference and habitat use. Body mass relative to canine size impacts killing ability (Donadio & Buskirk, 2006). Cats <20 kg are likely to consume small prey (<5 kg), except for the clouded leopard, which can take medium-sized prey with its relatively larger canines. Only Sumatran tigers take large prey. Longer tails relative to head and body length are thought to increase balance (Walker, Vierck & Ritz, 1998) enhancing tree climbing abilities and potentially use of steep terrain. Skills range from occasional climbing (tigers) to

Table 4 Provisional findings on possible mechanisms maintaining coexistence between cat species pairs

Cat species pairs		Possible mechanism					
		Geographic	Elevation	Vertical strata	Micro-habitat[a]	Active time	Prey size
Sumatran tiger	Clouded leopard	⊘	✓✓	✓✓✓	✓	✓✓	✓
Sumatran tiger	Golden cat	✓✓	✓✓	✓	✓	⊘	✓✓
Sumatran tiger	Marbled cat	⊘	✓	✓✓	✓	✓	✓✓✓
Sumatran tiger	Leopard cat	⊘	⊘	✓	✓✓	✓	✓✓✓
Clouded leopard	Golden cat	✓✓	✓	✓	✓	✓✓✓	✓
Clouded leopard	Marbled cat	⊘	⊘	⊘	⊘	✓✓✓	✓✓
Clouded leopard	Leopard cat	⊘	✓✓	✓	✓✓	✓✓	✓✓
Golden cat	Marbled cat	✓✓	✓	✓	✓	⊘	✓✓
Golden cat	Leopard cat	✓✓	✓✓✓	✓	✓✓	✓✓	✓✓
Marbled cat	Leopard cat	⊘	✓✓✓	✓	✓✓✓	✓✓✓	⊘

✓✓✓, most probable; ✓✓, very likely; ✓, likely; ⊘, unlikely.

[a] Including presence of other species.

extremely skillful climbing for hunting of arboreal prey (clouded leopards).

Cats, prey, other carnivores: comparison among sites

Listed from most to least photo-trapped, we found leopard cats, tigers, clouded leopards, marbled cats and golden cats. We did not trap fishing cats; however, these cats are known to be difficult to detect in camera traps even if they are present and must be specifically targeted, which we did not attempt in our study. We did not detect flat-headed cats although they are reported to inhabit peat swamps near Kerumutan/Kampar (Wilting *et al.*, 2010). We did survey areas near water, and hence the lack of flat-headed cats is concerning. It is possible that flat-headed cats' low density and possibly low preference for established trails hindered detection, but given that two sites are periodically inundated with water, we would expect the area to contain flat-headed cats and suggest that future survey efforts be directed specifically at flat-headed cats to determine their status. Failure to photograph tigers in Peranap and Kampar (despite seeing their sign) most likely relates to their low density and possibly high levels of human disturbance.

We documented highest cat diversity in Rimbang Baling (based only on camera traps) and Peranap (all sign considered). These areas have relatively high prey activity and low tiger detections, possibly facilitating expansion of smaller carnivores into these areas. During field sampling period, these sites were also part of a large, intact, lowland mineral soil forest, with contiguous habitat that may support a larger number of species (Ceballos & Brown, 1995; but also see Koh & Ghazoul, 2010 and Koh *et al.*, 2010). Additionally, Rimbang Baling and Peranap contain an altitudinal transition with more variation in terrain, potentially containing more niches.

All cats except golden cats inhabited a wide elevational range available in the study area. In pairwise comparisons, the smaller cats tended to be excluded from seemingly preferred relatively lower altitudes. Dominance of larger carnivores over smaller ones has been well documented (Palomares & Delibes, 1994; Kamler *et al.*, 2003; Donadio & Buskirk, 2006), and without very large prey such as gaur or wild buffalo in our study area, competition between tigers and clouded leopards is expected to be more intense. Our data tend to support the supposition that smaller species shift elevation upwards as we found clouded leopards at higher elevations than tigers, and golden cats, which overlap clouded leopard prey, at even higher elevation in the landscape. Perhaps elevational segregation, even over such a small scale of 6–460 m, among tigers, clouded leopards and golden cats, is used as a mechanism to avoid competition. The preference of clouded leopards for higher elevation is in line with the finding from a study in Thailand (Ngoprasert *et al.*, 2012). In contrast, cats of very small size and little dietary overlap with tigers, such as leopard cats, tended to inhabit prime habitat, relatively lower elevation with tigers. Interestingly, this distribution of species across different elevations was also found by Pusparini *et al.* (2014) in northern Sumatra.

Unlike cats, Malayan sun bears and civets did not seem to avoid tigers and had high trap rates regardless of tiger photo trap rate. Although similar to tigers in body mass, sun bears consume distinctly different food items (Servheen, Herrero & Peyton, 1999) and are also capable of climbing trees and utilizing other forest strata. Dholes, however, have similar prey preference as tigers (Wang & Macdonald, 2009) and hence potentially high dietary overlap with tigers. We found that, except in peatland, trap rate of dholes was low in areas with tigers, suggesting avoidance.

Habitat use models

Leopard cat site use was positively associated with photo-trap rate of tigers, whereas tiger site use was positively associated with trap rate of non-cat carnivores. These results likely indicate tolerance between these taxa rather than causal relationship, recognizing that there are many possible mechanisms the species can exploit to maintain coexistence such as through separation in food items. Based on the model, only tigers and leopard cats were negatively influenced by distance to protected area cores; however, leopard cats may easily coexist with tigers as they have little overlap in dietary needs. As a result, in areas dominated by both tigers and leopard cats, the mid-sized competitor might be excluded. Water-related variables did not increase cat use, perhaps because water is likely highly available across the landscape in other forms that are not picked up in the GIS analysis.

Closer proximity to roads increased tiger site use, contrary to our expectation, especially in light of the opposite findings from Kerinci-Seblat National Park (Linkie *et al*., 2006). Unlike Kerinci, however, which has a relatively intact, large forest block, our study area is more fragmented with forest blocks separated from each other by roads, plantations or settlements. This relationship may also largely be driven by the flat lowland forest of Tesso Nilo, which has the highest tiger density (Sunarto *et al*., 2013) and is surrounded by major public roads.

SIFs

Spatial and temporal co-occurrence

Spatially, we found little evidence of 'avoidance' interactions among cats. Rather, all cats occurred independently across specific camera locations. When SIF was estimated, it was always positive, indicating co-occurrence, not potential avoidance, but these models were not better than the models with the SIF set to 1.0 (independence). Lack of co-occurrence might result from data summarization on the coarse scale of 1-month time intervals for our encounter occasions. Unfortunately, our trap rates were too low to organize data into daily or weekly time frames, but higher trapping effort in future studies may permit such a fine scale analyses providing increased insight into spatial overlap. Additionally, habitat features likely also influence occupancy and detection, but we were unable to simultaneously model habitat variables within our co-occurrence models due to sample size constraints.

Encounter rates of clouded leopards, known to be active day and night, were lower during the day in our study. This may suggest more nocturnal activity, assuming that they do not become more active arboreally during the day and are simply missed by our terrestrial camera traps. Golden cats, also known to be active day and night, were primarily diurnal, resembling the pattern in Kerinci Seblat (Ridout & Linkie, 2009). Marbled cats are known to be primarily nocturnal in some studies (Nowell & Jackson, 1996; Grassman *et al*., 2005; Johnson, Vongkhamhenga & Saithongdam, 2009) and primarily diurnal by Johnson *et al*. (2009) and this study. Only tigers and leopard cats were consistent with the literature: tigers were active both day and night, while leopard cats were primarily nocturnal. Tigers had the lowest temporal activity overlap (Δ) with clouded leopards, the most likely competitor due to body size and prey overlap. This suggests that smaller cats adjust activity time or place to avoid larger cats. In fact, we found lower average temporal overlap between cat pairs most similar in body size ($\Delta = 0.62$) than between the cat next most distant in body size ($\Delta = 0.79$). This is supported by similar findings for wild cats in Thailand (Lynam *et al*., 2013). Interestingly, species of very different body sizes, yet inhabiting a similar guild such as clouded leopards and marbled cats (arboreal climbers), show the lowest temporal overlap of any species pair.

Mechanisms for coexistence

At the landscape scale, golden cats were most restricted, occurring only in the two most intact forest blocks and within those blocks, occurring at relatively higher elevation than any other species. Perhaps, segregation in habitat type and elevation are used to maintain coexistence. All other cats occurred in all forest types surveyed. However, marbled cats occurred at relatively higher elevation than the most similar-sized cat, the leopard cat. Temporal avoidance appeared to be exhibited by clouded leopards and golden cats, clouded leopards and marbled cats, and marbled cats and leopard cats. Clouded leopards and tigers likely used a combination of temporal avoidance and separation in use of vertical strata. However, either geographical/altitudinal or temporal occurrence patterns among cats may simply be a secondary by-product of higher numbers/activity in some areas due to other factors not addressed in this study such as variation in prey abundance or level of disturbance.

Management implications

To maintain cat diversity, in addition to protection of the species and their habitats, it would be beneficial to anticipate the effects of interspecific interactions, which might prevent a species from inhabiting certain areas or depress competitor numbers. In the lowlands of Tesso Nilo, for example, both tigers and leopard cats can live at high densities in lowland forest potentially leaving little space for other cats (consistent with our low trap rate of mid-sized cats in this area). Therefore, if other reserves at higher elevations or with alternative habitats are not available, smaller cats may have difficulty persisting. Compared with mainland Asia, Sumatran clouded leopards may be more nocturnal and live at much lower densities (Hutajulu *et al*., 2007; Hearn *et al*., 2008), especially when larger cat densities are high (Grassman *et al*., 2005). Arboreal forest habitat is needed to accommodate Sunda clouded leopard. Although small cats will survive with small-sized prey, large cats like tigers require prey (≥21.5 kg) larger than themselves due to energetic constraints (Carbone & Gittleman, 2002) and hence, tigers will need areas where levels of human activities, especially hunting for prey, are minimal (Sunarto *et al*., 2012, 2013). A study in Thailand found that prey was most important for tiger presence followed by habitat type (Ngoprasert *et al*., 2012).

Rimbang Baling and other lower slopes of hilly areas harbored five cat species. These areas provide large intact areas plus the habitat mosaic supporting the majority of the cat guild and its prey. However, some wetland specialists (fishing cats and flat-headed cats) were not found in our study. These cats might fare better in low productivity, peat swamp forests of Kerumutan and Kampar, even though these forests are unlikely to support high cat diversity or density. Further research for fishing cats and especially flat-headed cats should focus on investigating their occurrence in peatlands and wetlands of Sumatra because we do not currently understand their status and distribution or whether there are adequate protected areas to provide for conservation of these species.

The Tesso Nilo forest block is logged-over, isolated and has a mix of secondary forests. In much of Sumatra, however, lowland forests have either completely disappeared or remain in such a condition due to massive deforestation (Forest Watch Indonesia & Global Forest Watch, 2001; Holmes, 2002; Kinnaird *et al*., 2003; Uryu *et al*., 2007). The remaining forests, even degraded ones, still have high conservation value for wildlife (Linkie *et al*., 2008; Rayan & Mohamad, 2009) and even the critically endangered Sumatran tiger can achieve high abundance in such forests (Sunarto *et al*., 2013), likely because prey are still supported in these areas. Therefore, despite the widespread perception that rainforest animals need intact forest, we suggest that in addition to intact forested areas, protection of secondary, even degraded forests, is highly beneficial to maintaining the increasingly threatened wild cats in Sumatra.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. List of variables used to model the habitat use by cat species.
Appendix S2. Characteristics of Sumatran cat (sub)species based on literature from across the range of the species.
Appendix S3. Potential prey available in the study area as identified from camera trap pictures.