

Density and habitat use of the leopard cat (*Prionailurus bengalensis*) in three commercial forest reserves in Sabah, Malaysian Borneo

AZLAN MOHAMED,[†] RAHEL SOLLMANN,[†] HENRY BERNARD, LAURENTIUS N. AMBU, PETER LAGAN, SAM MANNAN, HERIBERT HOFER, AND ANDREAS WILTING*[†]

WWF–Malaysia, 49, Jalan SS23/15, 47400 Petaling Jaya, Selangor, Malaysia (AM)

Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Jalan UMS, 88400 Kota Kinabalu, Sabah, Malaysia (AM, HB)

North Carolina State University, Department of Forestry and Environmental Resources, Turner House Campus, Box 7646, Raleigh, NC, 27695-7646, USA (RS)

Sabah Wildlife Department, Wisma Muis, 88100 Kota Kinabalu, Sabah, Malaysia (LNA)

Sabah Forestry Department, Locked Bag 68, 90009 Sandakan, Sabah Malaysia (PL, SM)

Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Strasse 17, D-10315 Berlin, Germany (HH, AW)

* Correspondent: a.wilting@gmx.de

[†] Contributed equally.

The small (2- to 7-kg) leopard cat (*Prionailurus bengalensis*) is the most common cat species in Asia. Although it occurs in a wide range of habitats and seems to adapt well to anthropogenic habitat changes, surprisingly little is known about this species in the wild. All studies have focused on protected areas, although a large proportion of Southeast Asian forests are timber concessions. During this study, we used large camera-trapping data sets (783 records of 124 individuals) from 3 commercially used forests to investigate consequences of different logging regimes on density and habitat associations of the leopard cat. We applied spatial capture–recapture models accounting for the location of camera-traps (on or off road) to obtain estimates of leopard cat density. Density was higher in the 2 more disturbed forest reserves ($\bar{X} = 12.4$ individuals/100 km² \pm 1.6 SE and 16.5 \pm 2 individuals/100 km²) than in the sustainably managed forest (9.6 \pm 1.7 individuals/100 km²). Encounter rates with off-road traps were only 3.6–9.1% of those for on-road traps. Occupancy models, which accounted for spatial autocorrelation between sampling sites by using a conditional autoregressive model, revealed that canopy closure and ratio of climax to pioneer trees had a significantly negative impact on leopard cat occurrence. Our results confirm that the leopard cat is doing well in modified landscapes and even seems to benefit from the opening of forests. With such flexibility the leopard cat is an exception among tropical rain-forest carnivores.

Key words: camera-trapping, Felidae, logging concession, Southeast Asia, spatial capture–recapture models

© 2013 American Society of Mammalogists

DOI: 10.1644/11-MAMM-A-394.1

The Felidae is one of the best known mammalian families. However, most research to date has concentrated on larger felids, whereas the ecology of many small wild cats remains largely unknown. Most density estimates for smaller cats, if they are available at all, are drawn from radiotelemetry studies based on a limited number of individuals (e.g., Dillon and Kelly 2008; Dunstone et al. 2002; Rajaratnam 2000; Sliwa 2004). Only a few studies—most of which were restricted to small data sets—estimated densities of smaller cat species with camera-trapping data and capture–recapture models. Such estimates are restricted to the Americas (e.g., Reppucci et al. 2011; Trolle and Kéry 2003) and Europe (European wild cat [*Felis silvestris*; based on DNA—Kéry et al. 2011]); estimates

are not available for any African or Asian smaller cat species. Such a lack of information is not surprising for some of the rare small cats such as the flat-headed cat (*Prionailurus planiceps*) or the fishing cat (*Prionailurus viverrinus*), 2 endangered Southeast Asian cat species. However, this absence of basic demographic information also extends to more common felids.

One of these species is the leopard cat (*Prionailurus bengalensis*), the most common felid species in Asia, ranging from southern India to the Sunda Islands, including the



Philippines, and in the north to the Russian far east and the Japanese islands of Tsushima and Iriomote (Sanderson et al. 2008; Sunquist and Sunquist 2009). The leopard cat is among the smallest felids with weights of 1.7–7.1 kg, with cats from Russia being 2–3 times larger than Bornean leopard cats (Sunquist and Sunquist 2009). They feed mainly on rodents and other small prey species such as squirrels, birds, or reptiles (Grassman 1998; Rabinowitz 1990; Rajaratnam et al. 2007). Leopard cats occur from the lowlands to elevations > 3,000 m above sea level in the Himalayas (Ghimirey and Ghimire 2010) and are generally regarded as ground-dwelling.

Leopard cats are found in a broad range of habitat types from tropical lowland rain forests to coniferous forests in the Himalayas or Amur region. Leopard cats are not restricted to native habitats but also have been reported from logged forests, rubber estates, and oil palm plantations (Lim 1999; Rajaratnam et al. 2007). Because of its ability to adapt to different land cover types, the leopard cat is currently not considered as threatened and is classified by the International Union for Conservation of Nature as a species of “Least Concern” (Sanderson et al. 2008). However, the long-term threat of large-scale habitat modifications is difficult to assess, because the occurrence and abundance of the species in altered habitats remains unknown. Also, leopard cats are illegally traded throughout Asia because of the high demand for animal products (Shepherd and Nijman 2008).

Previous research on leopard cats focused on radiotracking in fully protected areas such as national parks, wildlife reserves, or sanctuaries (Sabah, Malaysian Borneo [Rajaratnam et al. 2007], Thailand [Austin et al. 2007; Grassman 1998, 2000; Grassman et al. 2005; Rabinowitz 1990], and Japan [Sakaguchi 1994]). No previous detailed study focused on commercially used forests. This is particularly surprising, because logging concessions cover a large proportion of the existing forests, especially within tropical Southeast Asia (e.g., Giam et al. 2011). These habitats are therefore likely important for the persistence of Southeast Asian wildlife (Giam et al. 2011).

During this study we estimated densities of leopard cats using spatial capture–recapture models applied to large camera-trapping data sets from 3 commercially used forests. This is the 1st study to use photographic capture–recapture techniques to estimate abundance and densities of leopard cats by the identification of individuals from their unique pelage patterns. In addition, we used occupancy models to identify habitat variables influencing the occurrence of the species. The main objective of this study was to investigate the resilience of the leopard cat to anthropogenic habitat modifications, specifically timber extraction, and thus, we discuss our results in the context of the different logging histories of our 3 study sites.

MATERIALS AND METHODS

Study areas.—We conducted camera-trap surveys in Deramakot Forest Reserve (DFR), Tangkulap-Pinangah Forest Reserve (TFR), and Segaliud Lokan Forest Reserve

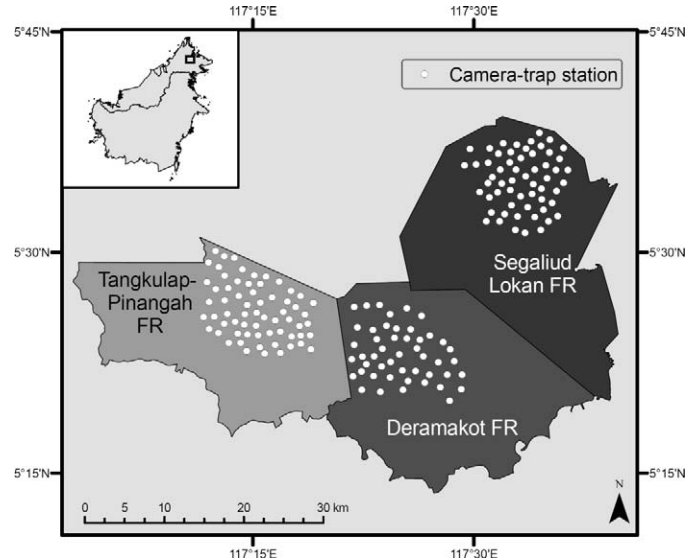


FIG. 1.—Location of the camera-trap stations within the 3 study areas in Sabah, Malaysian Borneo.

(SLFR). All study sites are located next to each other in the lowlands of central Sabah (Fig. 1), at altitudes between 50 and 250 m above sea level. During the last 50 years all areas have been repeatedly logged using different selective logging techniques. Today DFR (5°14–28°N, 117°19–36°E) and TFR (5°17–30°N, 117°11–21°E) are managed by the Sabah Forestry Department, whereas SLFR (5°20–27°N, 117°23–39°E) has been privately managed by KTS Plantation Sdn. Bhd. since 1994. In all forest reserves hunting is forbidden and oil palm plantations border the study areas to the north, as well as to the east for SLFR. DFR encompasses approximately 550 km² and is managed in accordance with sustainable forestry principles (Lagan et al. 2007). In 1997 it received certification from the Forest Stewardship Council. In contrast, TFR (501 km²) and SLFR (572 km²) were repeatedly logged using conventional selective logging techniques (see Wyatt-Smith [1995] for details) in the past. Consequently, forest structure is much more degraded than in DFR. Logging was ceased in TFR in 2001 and in June 2011 TFR also received certification from the Forest Stewardship Council. There are no plans to perform any logging activities within the next 2–3 decades to allow natural regeneration. In the 1st years after KTS Plantation took over the management of SLFR, parts of our study area were clear-cut and set aside for industrial tree plantation. However, the practices were revised in 1998 and since then reduced impact logging practices have been applied in SLFR. This forest reserve was certified by the Malaysian Timber Certification Scheme in 2009.

Camera-trapping.—We set up 47, 64, and 55 camera-trap stations, covering areas of 123 km², 122 km², and 114 km² in DFR, TFR, and SLFR, respectively (Fig. 1). Because of the limited number of camera-traps, we divided DFR and TFR into 3 and SLFR into 2 equal-sized blocks, which were sampled subsequently for 42 (DFR and TFR) or 48 (SLFR) consecutive days. Total sampling duration was approximately 4 months, a

period within the range of durations used in similar studies to approximate a closed population (e.g., Kawanishi and Sunquist 2004; Royle et al. 2011). DFR was sampled between September 2008 and January 2009, TFR between April and September 2009, and SLFR between January and April 2010. Because there are no strong seasonal differences in northeastern Borneo we do not expect the timing of the surveys to affect leopard cat densities. Leopard cats in Sabah move over home ranges between 2 and 5 km² (Rajaratnam et al. 2007). Camera stations were spaced approximately 1.7 km apart, ensuring that the trapping grid had no holes larger than an average home range, in order to expose all individuals within the grid to camera-traps. Each station consisted of 2 camera-traps (models Expert and Capture; Cuddeback, De Pere, Wisconsin) facing each other to capture both flanks of a passing animal. This setup permitted individual identification from photographs on the basis of their unique spot patterns. Individual leopard cats were identified independently by 2 persons; we discarded pictures that could not be identified unambiguously (e.g., blurry pictures or tails only). Sex of the animals was recorded whenever the photographs allowed visual identification.

Density estimates.—To estimate leopard cat density, we 1st constructed a spatial encounter history for each photographed individual by noting how many times it had been photographed at each station. We analyzed these data using spatial capture–recapture models (Efford 2004; Royle and Young 2008). These models take into account individual location and movement relative to the trapping grid by assuming that the number of times an individual i is detected at a trap j , λ_{ij} , decreases with increasing distance of j , d_{ij} , from the individual's home-range center. Spatial capture–recapture models contain a detection parameter, λ_0 (baseline trap encounter rate), and a movement parameter, σ (units of the trapping grid, here kilometers), controlling the shape of the decreasing function that relates λ_{ij} to d_{ij} . σ can be translated into a home-range radius assuming a bivariate normal model for movement (Reppucci et al. 2011). We allowed λ_0 to differ between roads and small forest trails, because most leopard cat pictures were taken at on-road cameras and other felids have been shown to preferably walk along, and thus have a higher detection probability on, roads (e.g., tigers [*Panthera tigris*—Karanth and Nichols 1998] and jaguars [*Panthera onca*—Sollmann et al. 2011]). We scaled λ_0 to 6-day occasions, so that it expressed the expected number of photographs per occasion. Because individual home-range size and movement behavior can vary among sites as a consequence of differences in resource availability, we analyzed each study site separately.

In spatial capture–recapture models, density is estimated as the number of individuals N in the state-space S , which is an area larger than, and encompassing, the trapping grid. S needs to be chosen large enough so as to contain all individuals that could have potentially been exposed to the trapping grid. To estimate N we used a Bayesian analysis by data augmentation (Royle et al. 2007). In data augmentation, we let M be a number that was larger than the largest possible population size

N in S , and n be the number of detected individuals. We assume a prior distribution for N that is uniform over the interval $(0, M)$ and augment the observed data set with $M - n$ individuals whose photographic encounter histories are all 0. N is then estimated as a fraction of M . We defined S as the outermost coordinates of each trapping grid plus a 7.5-km buffer, corresponding to areas of 778 km², 801 km², and 770 km² for DFR, TFR, and SLFR, respectively. Considering the average home-range size of leopard cats in similar areas (Rajaratnam et al. 2007) this buffer should be large enough so that S included all individuals potentially exposed to the trapping grid.

We implemented the spatial capture–recapture model in the program WinBUGS (Gilks et al. 1994) accessed through the software R (R Core Development Team 2011) with the package R2WinBUGS (Sturtz et al. 2005; see Appendix I for run specifications). We reported parameters as the posterior mean \pm standard error (SE) and the 5% and 95% quantile of the posterior distribution, which correspond to the 95% Bayesian credible interval (95BCI). We regarded parameters as significantly different from each other when the 95BCI of one did not contain the posterior mean of the other and vice versa.

Habitat surveys.—We characterized the habitat surrounding each camera-trap station to assess the general forest structure and disturbance within our 3 study areas. Three 250-m line transects were surveyed in the direction of 0°, 120°, and 240° and the data of the 3 transects were pooled. We collected information on canopy closure (CC) measured every 50 m using a spherical densitometer; number of climax (family Dipterocarpaceae) and pioneer (*Macaranga* spp. and *Mallotus* spp.) trees > 10 cm diameter at breast height (DBH) at a distance of 2 m from the transect line; and DBH of all trees > 10 cm at a distance of 2 m from the transect line. From these we computed the ratio of the number of climax to pioneer trees (rCP) and the ratio (rDBH) of large (DBH > 40 cm) to small trees (DBH < 10–20 cm). We expected all 3 variables (CC, rCP, and rDBH) to change with the degree of forest disturbance: less disturbed forests have a more closed canopy, a greater proportion of climax trees, and a higher proportion of young (10- to 20-cm-DBH) trees—indicating natural regrowth. We therefore tested for differences between the 3 study areas in each vegetation parameter using the nonparametric Jonckheere–Terpstra test for ordered alternatives, which makes full use of the information on the gradation of disturbance reported above (DFR less disturbed than TFR and TFR less disturbed than SLFR). Post hoc multiple comparisons were carried out using the Conover–Iman test (Conover 1999). For each site we also tested for the strength of association between all 3 habitat measures using Spearman rank correlation coefficients, ρ . All tests were carried out using the statistics software SYSTAT 13.0 (SYSTAT Software Inc., Chicago, Illinois).

Occupancy model.—To investigate habitat associations of the leopard cat we used occupancy models (MacKenzie et al. 2006). We divided our camera-trap sampling period into 6-day

TABLE 1.—Summaries of the results from spatial capture–recapture models of leopard cat (*Prionailurus bengalensis*) camera-trapping data from 3 forest reserves in Sabah, Malaysia.

Parameter ^a	Units	\bar{X}	SE	2.5%	Median	97.5%
Deramakot Forest Reserve (DFR)						
σ	km	2.018	0.113	1.816	2.013	2.254
λ_0	Photograph/occasion	0.629	0.082	0.486	0.624	0.805
ρ	—	0.080	0.025	0.040	0.077	0.136
D	Individual/100 km ²	9.558	1.663	6.685	9.385	12.984
Tangkulap-Pinangah Forest Reserve (TFR)						
σ	km	2.666	0.150	2.389	2.661	2.983
λ_0	Photograph/occasion	0.457	0.048	0.370	0.455	0.556
ρ	—	0.091	0.027	0.047	0.088	0.154
D	Individual/100 km ²	12.403	1.616	9.485	12.355	15.725
Segaliud Lokan Forest Reserve (SLFR)						
σ	km	3.352	0.192	3.010	3.343	3.758
λ_0	Photograph/occasion	0.620	0.101	0.452	0.611	0.850
ρ	—	0.036	0.011	0.018	0.035	0.062
D	Individual/100 km ²	16.500	1.997	12.992	16.370	20.657

^a σ = movement parameter; λ_0 = baseline trap encounter rate; ρ = multiplicative effect on λ_0 for off-road cameras; D = density.

occasions. We had a total of 7 occasions in DFR and TFR and 8 occasions in SLFR. We constructed a detection–nondetection matrix for all cameras and occasions, with an entry of 1 if a leopard cat had been detected at a particular camera and occasion, and an entry of 0 otherwise. In the occupancy models, each camera-trap station was characterized by the mean of CC, rCP, and rDBH. Assuming the leopard cat had similar associations with different habitat types across the 3 neighboring study sites, we joined data from all sites and modeled occupancy for this joint data set.

To reduce the number of candidate occupancy models, we applied a 2-stage model-building approach. We 1st held the occupancy probability Ψ constant and developed the most suitable model for detection probability p . We included an effect of p for camera-trap placement off roads, analogous to the spatial capture–recapture model. In addition, we tested whether p differed among study sites, so that the full detection model in its logit-linear form was:

$$\text{logit}(p) = a + b1(\text{DFR}) + b2(\text{TFR}) + b3(\text{off-road}),$$

where a corresponds to the on-road detection probability in SLFR; $b1(\text{DFR})$ and $b2(\text{TFR})$ represent the difference in p in DFR and TFR, respectively, and relative to SLFR; and $b3(\text{off-road})$ is the difference in detection at off-road cameras relative to on-road cameras. We retained significant site differences in the final model for p . We considered parameters as significant if their 95BCI did not include 0. Conditional on this detection model we separately modeled Ψ as a function of 1 of the 3 habitat variables. We only retained those variables that had a significant relationship with Ψ and combined significant variables in an additive model. We used the final model to estimate the number of sampling sites occupied by leopard cats at each study site.

Because of our sampling design, with a mean distance of only 1.7 km between camera-trap stations, and the mobility of the studied species, occupancy states are spatially autocorrelated (i.e., the state of occupancy at a given site is influenced by

the occupancy state of the sites nearby). To account for spatial autocorrelation, we added a random spatial effect e to the linear predictor of $\text{logit}(\Psi)$. Its value at site i , e_i , is conditional on the value of e at all sites in the neighborhood, corresponding to a conditional autoregressive model (Besag et al. 1991). We defined the neighborhood of each sampling site as all camera-traps within the radius of a leopard cat home range. We calculated this radius by converting the highest estimate of σ from the spatial capture–recapture model to a home-range radius. We implemented the model in a Bayesian framework (Royle and Dorazio 2008) in the program WinBUGS (see Appendix I for run specifications).

RESULTS

Camera-trapping.—Camera-traps in DFR, TFR, and SLFR accumulated 1916, 2,203, and 2,933 trap days, respectively. We obtained 178 records of 23 distinct leopard cats (11 males, 11 females, and 1 unidentified) in DFR, 287 records of 41 individuals (29 males, 6 females, and 6 unidentified) in TFR, and 318 records of 60 individuals (36 males, 4 females, and 20 unidentified) in SLFR.

Leopard cat density.—Baseline trap encounter rates λ_0 ranged from 0.456 ± 0.048 SE in TFR to 0.629 ± 0.082 in DFR (Table 1). Trap encounter rates for camera-traps located off roads were only 3.6–9.1% of those on roads. The movement parameter σ ranged from 2.018 ± 0.113 in DFR to 3.352 ± 0.192 in SLFR (Table 1). Leopard cat density was lowest in DFR, with $\bar{X} = 9.6$ individuals/100 km² ± 1.7 SE, followed by TFR with 12.4 ± 1.6 individuals/100 km², and SLFR with 16.5 ± 2.0 individuals/100 km² (Table 1).

Vegetation surveys.—Using Spearman rank correlation coefficients, there was little or modest correlation between the individual measures for CC, rCP, and rDBH within each study site. In DFR ($n = 47$), $\rho_{CC,rCP} = 0.33$, $\rho_{CC,rDBH} = 0.15$, and $\rho_{rCP,rDBH} = 0.15$; in TFR ($n = 60$), $\rho_{CC,rCP} = -0.12$, $\rho_{CC,rDBH} = -0.08$, and $\rho_{rCP,rDBH} = 0.39$; and in SLFR ($n = 57$),

TABLE 2.—Means and standard deviations (*SDs*) of habitat variables used in occupancy modeling for each study site. DFR = Deramakot Forest Reserve; TFR = Tangkulap-Pinangah Forest Reserve; SLFR = Segaliud Lokan Forest Reserve; DBH = diameter at breast height.

	\bar{X}			Global test ^a <i>P</i> -value	Post hoc comparisons ^b		
	DFR (<i>SD</i>)	TFR (<i>SD</i>)	SLFR (<i>SD</i>)		DFR–TFR	TFR–SLFR	DFR–SLFR
Canopy closure (CC)	0.849 (0.133)	0.655 (0.167)	0.562 (0.231)	< 0.001	< 0.001	0.026	< 0.001
Ratio no. climax/pioneer trees (rCP)	0.782 (0.235)	0.439 (0.252)	0.389 (0.296)	< 0.001	< 0.001	0.18	< 0.001
Ratio large/small trees (rDBH)	0.166 (0.112)	0.240 (0.156)	0.329 (0.197)	< 0.001	0.0048	0.0055	< 0.001

^a Jonckheere–Terpstra test for ordered alternatives.

^b Conover–Iman test for all pairwise comparisons.

$\rho_{CC,rCP} = -0.05$, $\rho_{CC,rDBH} = 0.04$, and $\rho_{rCP,rDBH} = -0.19$. All 3 habitat measures differed significantly between the study sites (Table 2). Pairwise comparisons between sites demonstrated significant differences for all comparisons for all 3 variables, with the exception that rCP was similar in TFR and SLFR (Table 2).

Leopard cat occupancy.—Habitat covariates were missing for 4 camera-trap sites each in TFR and SLFR; we excluded these sites from occupancy modeling. We detected leopard cats 90 times at 24 (51%) of the 47 camera-trap stations in DFR, 139 times at 47 (78%) of 60 stations in TFR, and 117 times at 33 (65%) of 51 stations in SLFR. The estimate of home-range radius for the largest σ was 5.8 km (in SLFR). We used this radius to determine the neighborhood of each camera-trap site in the conditional autoregressive occupancy model.

Leopard cat detection was significantly lower at off-road cameras and higher in DFR than TFR or SLFR, which were similar (Table 3). We therefore retained the road effect and different on-road detection in DFR in our final detection model.

Conditional on the detection model, both CC and rCP had a significantly negative effect on leopard cat occupancy (i.e., 95BCI of coefficient did not include 0). When combined in an

TABLE 3.—Parameter estimates from candidate models for detection and occupancy of leopard cat (*Prionailurus bengalensis*) in 3 forest reserves (Deramakot Forest Reserve [DFR], Tangkulap-Pinangah Forest Reserve [TFR], and Segaliud Lokan Forest Reserve [SLFR]) in Sabah, Malaysia. 95BCI = 95% Bayesian credible interval; CC = canopy closure; rCP = ratio of number of climax to pioneer trees; rDBH = ratio of trees with diameter at breast height > 30 cm to < 30 cm.

Model	Parameter	Estimate (<i>SE</i>)	95BCI	
Detection model ^a	$p(\text{road, site})$			
	$b1(\text{DFR})$	0.453 (0.220)	0.023, 0.881	
	$b2(\text{TFR})$	-0.012 (0.184)	-0.378, 0.342	
	$b3(\text{off-road})^*$	-2.309 (0.223)	-2.749, -1.865	
Occupancy models ^b	$\Psi(\text{CC})$	$b1(\text{CC})^*$	-3.065 (1.273)	-5.528, -0.837
	$\Psi(\text{rCP})$	$b1(\text{rCP})^*$	-0.745 (0.368)	-1.506, -0.058
	$\Psi(\text{rDBH})$	$b1(\text{rDBH})$	-0.171 (0.365)	-0.847, 0.598
	$\Psi(\text{rCP} + \text{CC})$	$b1(\text{CP})$	-0.645 (0.436)	-0.930, 0.201
		$b2(\text{CC})^*$	-2.059 (1.069)	-4.580, -0.542

^a Ψ is constant, and $b1(\text{DFR})$ and $b2(\text{TFR})$ express difference in on-road detection relative to SLFR.

^b Conditional on best detection model including a road effect and different detection in DFR.

* Parameter significant as 95BCI does not overlap 0.

additive model, rCP became marginally insignificant (Table 3). If only canopy closure was considered as influential on occupancy, then leopard cats occurred at a significantly lower percentage of camera-traps in DFR than SLFR and TFR, which were occupied to a similar extent (Table 4).

DISCUSSION

Our results are based on the largest camera-trapping data set analyzed so far for a small cat species. Among our 3 study sites we recorded 124 individual leopard cats 783 times; in SLFR alone we had 318 records of 60 individuals. As expected, leopard cats had much higher trap encounter rates at cameras installed along roads than at cameras set along small game trails. This suggests that, as for other felids, roads are preferable landscape structures on which to set up cameras for population studies of leopard cats. A factor favoring the use of roads by leopard cats might be local abundance of prey. During night spotlight surveys, leopard cats often were encountered along a stretch of grass next to logging roads (A. Mohamed and A. Wilting, pers. obs.). In addition, several times leopard cats were photographed along a road carrying their prey, a small rodent.

Because of the small size of leopard cats, identifying their sex, especially the unambiguous identification of females, is much more difficult than for larger cat species, and thus sex could not be determined for many individuals. Still, examination of our raw photographic data suggested that differences in σ and λ_0 between sexes exist. Individual female leopard cats were photographed much less frequently than males. This also

TABLE 4.—Estimates of detection probability *P* and percentage of camera-trap stations occupied (% occupied) from a model including an effect of trap placement (on-road or off-road) and study site—Deramakot Forest Reserve (DFR), versus Tangkulap-Pinangah Forest Reserve (TFR) and Segaliud Lokan Forest Reserve (SLFR)—on detection, and an effect of canopy closure on occupancy. 95BCI = 95% Bayesian credible interval.

Parameter	Site	Estimate (<i>SE</i>)	95BCI
<i>P</i> (on-road)	DFR	0.616 (0.041)	0.547, 0.694
	TFR, SLFR	0.488 (0.026)	0.447, 0.540
<i>P</i> (off-road)	DFR	0.181 (0.038)	0.123, 0.262
	TFR, SLFR	0.115 (0.021)	0.083, 0.161
% occupied	DFR	0.615 (0.049)	0.553, 0.745
	TFR	0.909 (0.027)	0.850, 0.967
	SLFR	0.755 (0.031)	0.726, 0.824

has been shown or suggested for other cat species (e.g., jaguars [Sollmann et al. 2011] and Sunda clouded leopards [*Neofelis diardi*—Wilting et al. 2012]). This is possibly caused by females having smaller home ranges, which has been shown previously in telemetry studies (e.g., Grassman 2000; Rajaratnam et al. 2007). Consistent with previous data (e.g., Rajaratnam 2000), leopard cats were predominantly nocturnal in all 3 study areas. Only 41 (5%) of all photographs were taken during the day (0600–1800 h).

We estimated moderate leopard cat densities in the commercially used forest reserves in our study, ranging from 9.6 individuals/100 km² in DFR to 16.5 individuals/100 km² in SLFR. The only other density estimate for Borneo was a minimum density of 37.5 individuals/100 km² based on the home ranges of 7 radiocollared individuals in Tabin Wildlife Reserve, Sabah (Rajaratnam 2000). However, the small sample size of the previous study and the different methodological approaches limit direct comparisons between the data sets. The relatively low densities of leopard cats are surprising, because within our study sites the species is generally assumed to be abundant (Sabah Forestry Department and KTS Plantation, pers. comm.). The fact that leopard cats use roads for movements increases the likelihood of people encountering this species. This could have led to the impression of a high density and highlights the importance of rigorous density estimations.

Leopard cat density was highest in SLFR followed by TFR and DFR. Although there are no data about leopard cat densities in the 3 study areas before logging activities commenced, our results indicate that density of this small cat is linked to habitat differences among the sites due to different logging histories. Habitat measures such as canopy closure, the ratio of climax to pioneer trees, and the ratio of larger to smaller trees can be interpreted as indicators for the degree of forest disturbance. In large parts of DFR the canopy was closed, with only a few gaps, whereas in TFR and especially in SLFR previous conventional selective logging activities resulted in more frequent and larger canopy gaps. Similarly, the ratio of climax to pioneer trees was highest in the well-managed forest reserve DFR and lowest in SLFR. Both habitat variables were significantly negatively associated with the probability of occurrence of leopard cats. This result is consistent with the observed variation in overall leopard cat densities and together both analyses suggest that leopard cats adapt well to forest disturbance and even seem to benefit from the opening of forests. Interestingly, within DFR none of the photographs of leopard cats was obtained from a camera-trap station along an animal trail under a closed forest canopy. This is in contrast to the results of other carnivores in tropical rain forests, which clearly prefer and sometimes even require a closed canopy (e.g., ocelot [*Leopardus pardalis*—Di Bitetti et al. 2008]).

Because the leopard cat is a strictly carnivorous species, its increasing density in more open habitats is most likely linked to higher prey availability in such habitats. The leopard cat is primarily a ground-dwelling species, although it has been

reported to rest high in the canopy (Rabinowitz 1990). Ecological studies in Thailand and Borneo suggest that the leopard cat mainly feeds on rodents, many of which are exclusively terrestrial (Grassman et al. 2005; Rabinowitz 1990; Rajaratnam 2000; Rajaratnam et al. 2007). It is generally known that small rodents benefit from closed understory vegetation and more complex understory vegetation structure (e.g., Drickamer 1990; Schmid-Holmes and Drickamer 2001). In more disturbed forests with frequent canopy gaps, understory vegetation is much thicker, whereas in undisturbed primary rain forests the forest floor is practically free of vegetation. Although we are not aware of any rodent abundance estimates from different habitats within Sabah, livetrapping data of small mammals in logged and unlogged forests showed that the number of captures of the 5 most common murids—the preferred prey species of leopard cats (Rajaratnam 2000)—was higher in disturbed forests than in an unlogged forest (Wells et al. 2007). Similarly, more individuals of common murids were captured in disturbed forests (M. Ancrenaz, pers. comm.). Although these capture frequencies do not necessarily reflect the absolute abundance of rodent species, they suggest that prey biomass for leopard cats might be higher in disturbed forests. We therefore expect that the density of leopard cats in a primary forest would be lower than in disturbed logged forests.

The structure of understory vegetation also could immediately benefit the leopard cat. As a terrestrial predator hunting by stealth, thick understory vegetation could provide more stalking cover and therefore increase hunting success. Thick vegetation also might provide the leopard cat with protection against larger sympatric predators.

Finally, most felids are sensitive to changing environments (e.g., ocelot [Di Bitetti et al. 2008] and flat-headed cat [Wilting et al. 2010]). It is conceivable that leopard cats also benefit from the decreasing abundance of other carnivores in disturbed habitats. Such an ecological (mesopredator) release (Crooks and Soulé 1999) was shown for the ocelot and other sympatric smaller cats (“ocelot-effect”) in South America (De Oliveira et al. 2010). Further studies from different areas are needed to understand the intraguild relationships among and the niche separation of carnivores in Southeast Asian rain forests.

Knowledge about the density and abundance of species and their ability to adjust to changing habitats is a key prerequisite for species conservation in rapidly changing environments. This study provides such an example for the leopard cat and supports the idea that this species prefers open forest habitats, possibly even disturbed ones, and therefore can do comparably well in altered landscapes. Although this is encouraging in terms of leopard cat persistence, there is cause for caution. It is still unknown which kind and degree of alterations the leopard cat tolerates. Many species, such as the orangutan (*Pongo pygmaeus*) in Sabah, tolerate habitat disturbance and densities may actually increase in secondary forests but if the habitat is altered too much their numbers greatly decline (Ancrenaz et al. 2005, 2010). Furthermore it is assumed leopard cats live in oil palm plantations because they are frequently encountered there.

However, such sightings must be treated with caution because it is unclear whether individuals are residents or merely in transit. Studies are needed to examine how far inside plantations leopard cats can survive, and whether individuals reside within or only travel into plantations from neighboring forests to forage. It is conceivable that leopard cats only use plantations for hunting during the night and that they require the forests for shelter and rest during the daytime. To fully assess the species' resilience to different forms of anthropogenic impact on habitat, long-term studies across a variety of different habitats are needed.

ACKNOWLEDGMENTS

We thank KTS Plantation Sdn. Bhd. and R. Alfred (formerly WWF–Malaysia) for their support, and the Sabah Economic Planning Unit for issuing a research permit. Financial support was provided by the following institutions: Point Defiance Zoo and Aquarium, Clouded Leopard Project, WWF–Germany, WWF–Malaysia, Cleveland Metroparks, Minnesota Zoo, Houston Zoo, Nashville Zoo, Panthera Foundation, Zoologische Gesellschaft für Arten und Populationsschutz (in English, Zoological Society for the Conservation of Species and Populations), and the Leibniz Institute for Zoo and Wildlife Research. AM is grateful for a personal scholarship of WWF–Malaysia and for a Russel Fellowship of WWF–United States. AW thanks the State of Berlin for the Elsa-Neumann stipend and the Deutsche Forschungsgemeinschaft for support (grant Fi-698/5-1). We thank B. Gardner for insightful discussions about the applied modeling approaches.

LITERATURE CITED

- ANCRENAZ, M., ET AL. 2005. Aerial surveys give new estimates for orangutans in Sabah, Malaysia. *PLoS Biology* 3:e3.
- ANCRENAZ, M., ET AL. 2010. Recent surveys in the forests of Ulu Segama Malua, Sabah, Malaysia, show that orang-utans (*P. p. morio*) can be maintained in slightly logged forests. *PLoS ONE* 5:e11510.
- AUSTIN, S. C., M. E. TEWES, L. I. GRASSMAN, JR., AND N. J. SILVY. 2007. Road ecology of the leopard cat *Prionailurus bengalensis* in Khao Yai National Park, Thailand. *Acta Zoologica Sinica* 53:373–377.
- BESAG, J., J. YORK, AND A. MOLLIE. 1991. Bayesian image restoration, with two applications in spatial statistics. *Annals of the Institute of Statistical Mathematics* 43:1–20.
- CASELLA, G., AND E. I. GEORGE. 1992. Explaining the Gibbs sampler. *American Statistician* 46:167–174.
- CONOVER, W. J. 1999. *Practical nonparametric statistics*. 3rd ed. John Wiley & Sons, Chichester, United Kingdom.
- CROOKS, K. R., AND M. E. SOULÉ. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563–566.
- DE OLIVEIRA, T., ET AL. 2010. Ocelot ecology and its effect on the small-felid guild in the lowland Neotropics. Pp. 559–580 in *Biology and conservation of wild felids* (D. W. Macdonald and A. J. Loveridge, eds.). Oxford University Press, Oxford, United Kingdom.
- DI BITETTI, M. S., A. PAVIOLO, C. D. DE ANGELO, AND Y. E. DI BLANCO. 2008. Local and continental correlates of the abundance of a Neotropical cat, the ocelot (*Leopardus pardalis*). *Journal of Tropical Ecology* 24:189–200.
- DILLON, A., AND M. J. KELLY. 2008. Ocelot home range, overlap and density: comparing radio telemetry with camera trapping. *Journal of Zoology* 275:391–398.
- DRICKAMER, L. C. 1990. Microhabitat preferences of two species of deermice *Peromyscus* in a northeastern United States deciduous hardwood forest. *Acta Theriologica* 35:241–252.
- DUNSTONE, N., ET AL. 2002. Spatial organization, ranging behaviour and habitat use of the kodkod (*Oncifelis guigna*) in southern Chile. *Journal of Zoology (London)* 257:1–11.
- EFFORD, M. 2004. Density estimation in live-trapping studies. *Oikos* 10:598–610.
- GELMAN, A., J. B. CARLIN, H. S. STERN, AND D. B. RUBIN. 2004. *Bayesian data analysis*. 2nd ed. CRC/Chapman & Hall, Boca Raton, Florida.
- GELMAN, A., AND J. HILL. 2006. *Data analysis using regression and multilevel/hierarchical models*. 1st ed. Cambridge University Press, New York.
- GHIMIREY, Y., AND B. GHIMIRE. 2010. Leopard cat at high altitude in Makalu-Barun National Park, Nepal. *Cat News* 52:16–17.
- GIAM, X., G. R. CLEMENTS, S. A. AZIZ, K. Y. CHONG, AND J. MIETTINEN. 2011. Rethinking the 'back to wilderness' concept for Sundaland's forests. *Biological Conservation* 144:3149–3152.
- GILKS, W. R., A. THOMAS, AND D. J. SPIEGELHALTER. 1994. A language and program for complex Bayesian modelling. *Journal of the Royal Statistical Society, Series D. The Statistician* 43:169–177.
- GRASSMAN, L. I., JR. 1998. Movements and prey selection of the leopard cat (*Prionailurus bengalensis*) in a subtropical evergreen forest in southern Thailand. *Societa Zoologica "La Torbiera"* 4:9–21.
- GRASSMAN, L. I., JR. 2000. Movement and diet of the leopard cat *Prionailurus bengalensis* in a seasonal evergreen forest in south-central Thailand. *Acta Theriologica Scientific Report* 45:421–426.
- GRASSMAN, L. I., JR., M. E. TEWES, N. J. SILVY, AND K. KRETIYUTANONT. 2005. Ecology of three sympatric felids in a mixed evergreen forest in north-central Thailand. *Journal of Mammalogy* 86:29–38.
- KARANTH, K. U., AND J. D. NICHOLS. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852–2862.
- KAWANISHI, K., AND M. E. SUNQUIST. 2004. Conservation status of tigers in a primary rainforest of Peninsular Malaysia. *Biological Conservation* 120:329–344.
- KÉRY, M., B. GARDNER, T. STOECKLE, D. WEBER, AND J. A. ROYLE. 2011. Use of spatial capture–recapture modeling and DNA data to estimate densities of elusive animals. *Conservation Biology* 25:356–364.
- LAGAN, P., S. MANNAN, AND H. MATSUBAYASHI. 2007. Sustainable use of tropical forests by reduced-impact logging in Deramakot Forest Reserve, Sabah, Malaysia. *Ecological Resources* 22:414–421.
- LIM, B. L. 1999. The distribution, food habits and parasite patterns of the leopard cat (*Prionailurus bengalensis*) in Peninsular Malaysia. *Journal of Wildlife and Parks* 17:17–27.
- MACKENZIE, D. I., J. D. NICHOLS, J. A. ROYLE, K. H. POLLOCK, L. L. BAILEY, AND J. E. HINES. 2006. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Academic Press, London, United Kingdom.
- RABINOWITZ, A. 1990. Notes on the behavior and movements of leopard cats, *Felis bengalensis*, in a dry tropical forest mosaic in Thailand. *Biotropica* 22:397–403.
- RAJARATNAM, R. 2000. Ecology of the leopard cat (*Prionailurus bengalensis*) in Tabin Wildlife Reserve, Sabah, Malaysia. Ph.D. dissertation, Universiti Kebangsaan Malaysia, Bangi, Malaysia.
- RAJARATNAM, R., M. SUNQUIST, L. RAJARATNAM, AND L. AMBU. 2007. Diet and habitat selection of the leopard cat (*Prionailurus bengalensis borneoensis*) in an agricultural landscape in Sabah, Malaysian Borneo. *Journal of Tropical Ecology* 23:209–217.

- R DEVELOPMENT CORE TEAM. 2011. Version 2.13.0. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- REPUCCI, J., B. GARDNER, AND M. LUCHERINI. 2011. Estimating detection and density of the Andean cat in the high Andes. *Journal of Mammalogy* 92:140–147.
- ROYLE, J. A., AND R. M. DORAZIO. 2008. Hierarchical modeling and inference in ecology. Academic Press, London, United Kingdom.
- ROYLE, J. A., R. M. DORAZIO, AND W. A. LINK. 2007. Analysis of multinomial models with unknown index using data augmentation. *Journal of Computational and Graphical Statistics* 16:67–85.
- ROYLE, J. A., A. J. MAGOUN, B. GARDNER, P. VALKENBURG, AND R. E. LOWELL. 2011. Density estimation in a wolverine population using spatial capture–recapture models. *Journal of Wildlife Management* 75:604–611.
- ROYLE, J. A., AND K. V. YOUNG. 2008. A hierarchical model for spatial capture–recapture data. *Ecology* 89:2281–2289.
- SAKAGUCHI, N. 1994. Ecological aspects and social system of the Iriomote cat *Felis iriomotensis* (Carnivora; Felidae). Ph.D. dissertation, Kyushu University, Fukuoka, Japan.
- SANDERSON, J., ET AL. 2008. *Prionailurus bengalensis*. In: IUCN 2011. IUCN Red list of threatened species. Version 2011.2. www.iucnredlist.org. Accessed 2 November 2011.
- SCHMID-HOLMES, S., AND L. C. DRICKAMER. 2001. Impact of forest patch characteristics on small mammal communities: a multivariate approach. *Biological Conservation* 99:293–305.
- SHEPHERD, C. R., AND V. NIJMAN. 2008. The wild cat trade in Myanmar. TRAFFIC Southeast Asia, Selangor, Malaysia.
- SLIWA, A. 2004. Home range size and social organisation of black-footed cats. *Mammalian Biology* 69:96–107.
- SOLLMANN, R., ET AL. 2011. Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguar in central Brazil. *Biological Conservation* 144:1017–1024.
- STURTZ, S., U. LIGGES, AND A. GELMAN. 2005. R2WinBUGS: a package for running WinBUGS from R. *Journal of Statistical Software* 12:1–16.
- SUNQUIST, M. E., AND F. C. SUNQUIST. 2009. Family Felidae (cats). Pp. 54–169 in *Handbook of the mammals of the world. Vol. 1. Carnivores* (D. E. Wilson and R. A. Mittermeier, eds.). Lynx Edicions, Barcelona, Spain.
- TROLLE, M., AND M. KÉRY. 2003. Estimation of ocelot density in the Pantanal using capture–recapture analysis of camera-trapping data. *Journal of Mammalogy* 84:607–614.
- WELLS, K., E. K. V. KALKO, M. B. LAKIM, AND M. PFEIFFER. 2007. Effects of rain forest logging on species richness and assemblage composition of small mammals in Southeast Asia. *Journal of Biogeography* 34:1087–1099.
- WILTING, A., ET AL. 2010. Modelling the species distribution of flat-headed cats (*Prionailurus planiceps*), an endangered south-east Asian small felid. *PLoS ONE* 5:e9612.
- WILTING, A., ET AL. 2012. Density of the Vulnerable Sunda clouded leopard *Neofelis diardi* in two commercial forest reserves in Sabah, Malaysian Borneo. *Oryx* 46:423–426.
- WYATT-SMITH, J. 1995. Manual of Malayan silviculture for inland forest. 2nd ed. Malayan Forest Records 23. Forest Research Institute Malaysia, Kepong, Malaysia. Vol. I.

Submitted 26 November 2011. Accepted 7 August 2012.

Associate Editor was I. Suzanne Prange.

APPENDIX I

Run specifications for spatial capture–recapture and occupancy models in WinBUGS

WinBUGS uses Gibbs sampling, a Markov chain Monte Carlo method simulating samples from the joint posterior distribution of the unknown quantities in a statistical model (Casella and George 1992). Markov chain Monte Carlo chains are started at arbitrary parameter values and because successive iterations depend on the outcome of the previous iteration, the start value will be reflected in a number of initial iterations that should be discarded (the burn-in). This characteristic also can lead to autocorrelation of successive iterations. To reduce autocorrelation, a thinning rate is specified as every i th iteration used in the characterization of the posterior distribution of the parameters.

We ran the spatial capture–recapture model for 20,000 iterations, with a burn in of 15,000, with 3 chains and a thinning rate of 3. For the occupancy model we used 3 chains with 30,000 iterations, a burn-in of 10,000, and a thinning rate of 3. This combination of values ensured an adequate number of iterations to characterize the posterior distributions, that Markov chain Monte Carlo chains showed no effects of the initial values, and that all chains converged (i.e., oscillated around essentially the same mean parameter value). We checked for chain convergence using the Gelman–Rubin statistic (Gelman et al. 2004), \hat{R} , which compares between and within chain variation. \hat{R} values below 1.1 indicate convergence (Gelman and Hill 2006). Values for all estimated parameters were below 1.1, with the exception of the location of 3 activity centers in the spatial capture–recapture model for Tangkulap-Pinangah Forest Reserve. In these cases, plotting the estimated locations revealed that the model was unable to place the respective individuals at either side of the only trap they had been captured in. This does not influence other model parameter estimates.