

Occurrence of Three Felids across a Network of Protected Areas in Thailand: Prey, Intraguild, and Habitat Associations

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ABSTRACT

Clouded Leopard, Leopard, and Tiger are threatened felids in Southeast Asia, but little is known about the factors influencing their distributions. Using logistic regression, we assessed how habitat variables, prey detection patterns, and presence of intraguild predators affect the occurrence of these felids across 13 protected areas within Thailand. Our analysis is based on data from 1108 camera-trap locations (47,613 trap-nights). Clouded Leopard and Leopard are associated with habitat where Red Muntjac and Eurasian Wild Pig were most likely to be present. Tiger are associated with habitat with a higher likelihood for the presence of Gaur, Eurasian Wild Pig, and Sambar. Clouded Leopard and Tiger were both weakly associated with areas with mature evergreen forest. Besides availability of prey, associations with potential competitors also appear to influence the distribution of these felids, although the strength of these effects requires further investigation. Occurrence rates for Clouded Leopard were no different in protected areas with Leopard versus without Leopards. Leopard had similar occurrence rates regardless of the presence of Tiger, but Leopards were less likely to be detected at the same camera-trap points with the larger felid. Our results suggest that the two most commonly photographed prey species in the study areas serve as key prey species, Eurasian Wild Pig for all three carnivores and Red Muntjac for Leopard and Clouded Leopard.

Abstract in Thai is available in the online version of this article.

Key words: carnivore conservation; interspecific interactions; *Neofelis nebulosa*; *Panthera pardus*; *Panthera tigris*; species distribution models.

UNDERSTANDING THE FACTORS DETERMINING THE ABUNDANCE AND PATTERNS OF HABITAT USE by animal species of conservation interest is integral to their management by, for example, informing habitat restoration projects (e.g., Xi *et al.* 2008, Trisurat *et al.* 2010), providing suitable areas for translocation or reintroduction (e.g., Fernández *et al.* 2006, Klar *et al.* 2008, Cook *et al.* 2010), or examining potential connections among suitable habitat patches (e.g., Muntiferung *et al.* 2006, Trisurat *et al.* 2010). It may also be possible to predict favored prey items of carnivores by looking for associations between the presence or density of the carnivore and the presence or density of one or more potential prey species (Karanth *et al.* 2004).

It is urgent that we assess the factors impacting the distribution of top predators. Top predators have been in decline over the last century due to a combination of habitat loss and fragmentation, loss of their prey base, and direct persecution (Karanth & Chellam 2009, Lynam 2010, Oswell 2010). Top predators often serve as keystone species and have been shown to be critical in structuring ecosystems (e.g., Terborgh *et al.* 2001, Johnson *et al.* 2007, Beschta & Ripple 2009, Ritchie & Johnson 2009). In addition, top predators can serve as excellent umbrella species in conservation planning (Sergio *et al.* 2008) because of their large home range sizes, overlap with other species of conservation concern, and sensitivity to forest degradation (e.g., Morrison *et al.* 2007).

We use data collected since 1997 from 13 different protected areas to assess potential factors affecting the distribution of the Tiger (*Panthera tigris*), Leopard (*Panthera pardus*), and Clouded

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Leopard (*Neofelis nebulosa*) across Thailand. These are the three largest felids in Southeast Asia, weighing on average approximately 155 kg and 110 kg, 50 kg and 35 kg, and 18 kg and 13 kg for males and females of each species, respectively (Silva & Downing 1995, Francis 2001, Grassman *et al.* 2005). Despite the difference in size between the three species, we expect substantial overlap in the range of prey sizes killed by Tiger and Leopard and between Leopard and Clouded Leopard (*e.g.*, Seidensticker 1976, Johnsingh 1992, Karanth & Sunquist 1995). Thus, competition among at least some pairs of the three felids is possible and could be an important factor affecting the overall distribution or occupancy of the three carnivores.

Our goals were to: (1) identify environmental factors associated with the current distribution of the three largest felids across selected sites in Thailand; (2) identify the prey species with which these felids were most closely associated; and (3) examine the potential for interactions among the three felids.

METHODS

Camera-trap data were collected from 13 protected areas within Thailand (Fig. S1; Tables 1 and S1). Surveys were conducted between April 1997 and July 2010. Camera traps were set at 1108 locations across the 13 protected areas. The mean number of trap-nights per camera was 45.6. Elevation of camera locations ranged from 49 to 1351 m (mean = 469 m). All sites were in protected areas, as all remaining suitable habitat for large carnivores in Thailand lies exclusively inside them. Hunting, a primary threat to large carnivores and their ungulate prey, is prohibited in all protected areas, although enforcement against poaching is highly variable among locations (Albers & Grinspoon 1997, Steinmetz *et al.* 2010a). The number of photographs for each species and the number of camera-trap locations where the species was detected are listed in Tables 1 and S1.

Objectives and methods varied among studies as did camera spacing (Table 1). Cameras were placed in areas with a high probability of being used by target animals, which were typically large carnivores (*e.g.*, trails, near water sources). We did not measure microhabitat variables along trails near the camera locations, although it is possible that such variables can influence detection rates of predators and their prey (Harmsen *et al.* 2010). Cameras were operational 24 h per d. Camera-trap locations were not baited and trail-cameras were secured to trees. Investigators checked their cameras every 7–14 d. We did not include data for which functioning cameras were left in the forest for fewer than 6 d. Greater than 98 percent of animal photos were submitted to an external expert and committee of experienced field researchers for species validation.

DATA ANALYSIS.—We used multiple logistic regression to examine associations between various abiotic and biotic factors (the independent variables) and detection/nondetection of the selected species (the dependent variable). We then employed an information-theoretic approach (AIC_c) to choose the model with the highest likelihood value and to weight (through model averaging)

TABLE 1. Data for each of the 13 study sites including number of locations with a trail camera (Camera Locations), total number of trap-nights for all locations (Trap-Nights), average distance between camera locations (D), and number of photos for Leopard (L), Clouded Leopard (CL) and Tiger (Tiger).

| Study site | Camera locations | Trap-nights | D | L | CL | Tiger |
|--------------------------------------------|------------------|-------------|-----|-----|----|-------|
| Bang Lang National Park (BL) | 14 | 463 | 1.2 | 0 | 4 | 17 |
| Hala Bala Wildlife Sanctuary (HB) | 29 | 10,879 | 2.8 | 2 | 6 | 9 |
| Huai Kha Kaeng Wildlife Sanctuary (HKK) | 173 | 1280 | 1.9 | 87 | 3 | 38 |
| Kaeng Krachan National Park (KK) | 94 | 7699 | 0.6 | 227 | 0 | 20 |
| Khao Ang Rue Nai Wildlife Sanctuary (KARN) | 252 | 5710 | 0.5 | 0 | 11 | 0 |
| Khao Sok National Park (KOS) | 1 | 9 | NA | 0 | 0 | 0 |
| Khao Yai National Park (KY) | 358 | 12,323 | 0.9 | 0 | 47 | 10 |
| Klongsaeng Wildlife Sanctuary (KLS) | 6 | 113 | 2.1 | 0 | 0 | 0 |
| Kuiburi National Park (KB) | 48 | 2511 | 0.7 | 23 | 0 | 11 |
| Phu Khieo Wildlife Sanctuary (PK) | 51 | 1212 | 0.6 | 0 | 6 | 6 |
| Ta Phraya National Park (TAP) | 22 | 677 | 2.6 | 2 | 11 | 0 |
| Thap Lan National Park (THP) | 6 | 187 | 1.8 | 0 | 0 | 0 |
| Thungyai Naresuan Wildlife Sanctuary (TY) | 53 | 4550 | 0.7 | 1 | 1 | 19 |

the relative importance of the different predictor variables (Burnham & Anderson 2002). Model averaging is preferred when, as in this case, multiple models were often reasonable fits to the data. The abiotic factors included distance to forest edge (*Edge*), elevation (*Elev*), habitat type (*Habitat*), distance to nearest unsealed (open to the public) road or village (*Human*), slope (*Slope*), average rainfall during the driest month (*Rain*), and distance to nearest river or stream (*Water*). All independent variables were log₁₀ transformed with the exception of Rain and Slope. All habitat variables had pairwise correlations coefficients <0.25 after transformation.

Habitat was converted to a continuous variable by multiplying mean tree density by mean basal area for eight habitat types that were encountered in camera-trap study areas: grassland/savanna, secondary forest, bamboo forest, mixed deciduous forest, dry dipterocarp forest, hill evergreen forest, moist evergreen forest, and dry evergreen forest. Input values were obtained from, and averaged across, numerous botanical studies conducted in the same protected areas as our camera trapping (for details of sources, see Supporting Information).

Abiotic factors were generated using ArcMap v.9.3 (ESRI, Redlands, California, U.S.A.). Shape files of habitat type, road, village, and stream were provided by the Thailand Department of National Parks, Wildlife, and Plant Conservation. Elevation data were derived from the ASTER Global Digital Elevation Model (<http://www.jspacesystems.or.jp/ersdac/GDEM/E/>). Slope data were calculated from the elevation data. Average rainfall during the driest month was collected from rain gage stations throughout Thailand between 1997 and 2008 and was provided by the Thailand Meteorological Department. Rainfall for each specific camera-trap location was interpolated using kriging (Kitanidis 1997).

Success of the logistic regression models was judged using receiver operating characteristic (ROC) plots (Fielding & Bell 1997). The area under the ROC curve (AUC) is a measure of overall fit and varies from 0.5 (for a model that does no better than random) to 1.0 for a perfect fit. Although some have been critical of using AUC when comparing the fit of models (e.g., Lobo *et al.* 2008), AUC is thought to be especially appropriate when comparing different models using the same data (Fielding & Bell 1997). We do not, however, rely solely on AUC as a measure of overall fit. We also rely on the model averaged AIC_c values, the traditional significance levels from the logistic regression, and sensitivity and specificity in the ROC curve (as suggested by Lobo *et al.* 2008) where appropriate.

We used logistic regression, instead of occupancy modeling, as our primary form of data analysis because estimates of occupancy rates may be heavily biased by the nonrandom sampling of only parts of protected areas and because of the likely violation of closure over such a long sampling period. The weakness of logistic regression is that absences may be due to a lack of detection and not a true absence (MacKenzie *et al.* 2002). In addition to the *national model* using all 1108 cameras as independent data points, a *fifty and over model* was constructed using only the 220 camera-trap locations where the camera spent ≥ 50 continuous trap-nights in the forest (mean = 123.1). Fifty continuous trap-nights is approximately the amount of time we calculate, from this data, to be at least 95 percent certain of capturing even the least common target species should it occur at that location. Thus, this model should greatly ameliorate problems associated with false absences.

In addition to the three models described above, we built models for the three individual protected areas with the largest data sets. The following individual protected areas were modeled, where N is the number of camera locations: HKK ($N = 173$), KK ($N = 94$), and KY ($N = 358$). These are subsets of the *national model*.

The raw proportion of camera-trap locations that detected a species gives an index of its occurrence at a site. To quantify associations between the three felids, we performed correlation analysis on the occurrence of Clouded Leopards, Leopards, and Tigers. Furthermore, to specifically test whether the presence of Leopards in a protected area potentially impacted the occurrence of Clouded Leopards, we performed a t -test comparing mean

occurrence of Clouded leopards in protected areas with and without Leopards.

MODEL BUILDING PROCEDURES.—Logistic regression in combination with AIC_c was used to determine the relative importance of the abiotic factors: *Edge*, *Elev*, *Habitat*, *Human*, *Rain*, *Slope*, and *Water* for each of the three carnivores. After building models using only abiotic factors, a global model was constructed using abiotic and biotic factors. The additional biotic factors were *Prey* (defined below) and a potential competitor. For Clouded Leopards, detection or nondetection of Leopards was entered into the model as a binary variable, whereas for Leopards, the detection or nondetection of tigers was included in the model as a binary variable.

Logistic regression was used to build models for potential prey species using the seven abiotic factors. The output produced from the logistic regression models for prey was solved to produce continuous-probability values ranging from 0.0 to 1.0. The higher values indicate a higher probability of occurrence. The probabilities for each prey species at each camera location were then entered as independent variables into a logistic regression to see which, if any, of the potential prey species were associated with detection of the predator. The species tested for associations were based on numerous published accounts of diet. Potential prey for Clouded Leopard and Leopard were Hog Badger (*Arctonyx collaris*), Red Muntjac (*Muntiacus muntjac*), Sambar (*Rusa unicorn*), and Eurasian Wild Pig (*Sus scrofa*). For Tigers, Hog Badger was replaced with Gaur (*Bos gaurus*). An information-theoretic approach, corrected for small sample sizes (AIC_c), was then employed to choose which species to keep in a final model. To avoid having models for prey that contained only one habitat variable (and therefore completely collinear with it), we kept the prey model with the lowest AIC_c value that contained at least two habitat variables. This final linear equation was specific to each carnivore and treated as an explanatory variable (*Prey*) in further model building.

Correlation coefficients between Prey and the abiotic variables were generally small (<0.40). The overall accuracy of the models was measured using AUC and the relative importance of each factor was determined using the information-theoretic paradigm and model averaging (Burnham & Anderson 2002). Analyses were carried out using JMP software v.8 (SAS Institute, Cary, North Carolina, U.S.A.).

RESULTS

The *national model* consistently performed better than the *fifty and over model* (Table S2). For all three species the predictor variables chosen were nearly identical between the two models. Resampling statistics (Table S2), which includes a measure of model uncertainty, also shows the *national model* performing best for all three predator species. This is consistent with Tyre *et al.* (2003), who suggested that when error rates are <50 percent, greater efficiency is gained by adding more sites rather than more sampling periods; and that the logistic regression will converge on the true species–habitat relationships as samples size becomes very large.

All models including both abiotic and biotic factors, at the national level and the level of individual protected areas, produced results that were significantly different from random (AUC > 0.50; Tables 2 and 3). The overall logistic regression models were also highly significant using conventional significance testing (Chi-square test, $P < 0.001$). The prey models were not a direct goal of this study, but rather a means of building a better predator model. Thus, the prey models and their details have been placed in Table S3. The prey models ranged from poor to excellent, but most were considered adequate (AUC = 0.70–0.80).

PREY ASSOCIATIONS.—The associations between felids and potential prey were highly consistent. Using prey alone produced poor to good models, with most models being considered adequate (AUC = 0.70–0.80). Clouded Leopards were most closely associated with places where Red Muntjac and Eurasian Wild Pig occurred (Table 2). Leopards also were most closely associated with places with Eurasian Wild Pig and Red Muntjac, although there was also evidence for weaker correlations with Hog Badger and Sambar (Table 2). Presence of tigers was associated with Gaur, Eurasian Wild Pig, and Sambar (Table 2).

HABITAT ASSOCIATIONS.—The associations between felids and abiotic factors produced adequate models (AUC = 0.70–0.80), but all improved to good (AUC = 0.80–0.90) when biotic factors were added (Tables 3 and S4). For Clouded Leopard and Tiger, the abiotic factors identified as important were similar whether

TABLE 2. Prey species and their relative importance values for *Neofelis nebulosa*, *Panthera pardus*, and *Panthera tigris*. Model denotes whether it was the model for all of Thailand (National) or for a particular protected area. The importance values were determined using AIC_c and model averaging. Importance values were scaled so that the most important prey species had a value of 1.00, and all other prey species' importance values are given relative to it. AUC represents a measure of model success relative to a random model (AUC = 0.50).

| Model | Prey species included | AUC |
|--------------------------|-----------------------------------------------------------------|------|
| <i>Neofelis nebulosa</i> | | |
| National | Red Muntjac (1.00), Eurasian Wild Pig (1.00) | 72.8 |
| HKK | Red Muntjac (1.00), Eurasian Wild Pig (0.97) | 62.3 |
| KY | Hog Badger (1.00), Red Muntjac (0.90) | 70.5 |
| <i>Panthera pardus</i> | | |
| National | Hog Badger (1.00), Red Muntjac (0.73), Eurasian Wild Pig (0.42) | 73.2 |
| HKK | Sambar (1.00), Eurasian Wild Pig (0.95), Red Muntjac (0.71) | 60.8 |
| KK | Eurasian Wild Pig (1.00), Red Muntjac (0.56) | 81.5 |
| <i>Panthera tigris</i> | | |
| National | Gaur (1.0), Eurasian Wild Pig (1.0), Sambar (0.36) | 79.4 |
| HKK | Sambar (1.00), Gaur (0.96), Eurasian Wild Pig (0.78) | 60.4 |
| KK | Eurasian Wild Pig (1.00), Sambar (0.63), Gaur (0.35) | 62.6 |
| KY | Gaur (1.00), Eurasian Wild Pig (0.64), Sambar (0.28) | 79.0 |

TABLE 3. Abiotic and biotic variables and their relative importance values (in parentheses) for Clouded Leopard (*Neofelis nebulosa*), Leopard (*Panthera pardus*), and Tiger (*Panthera tigris*). Model denotes whether it was the model for all of Thailand (National) or for a particular protected area. The importance values were determined using AIC_c and model averaging. Importance values were scaled so that the most important variables had a value of 1.00 and all other variables were relative to the most important. AUC represents a measure of model accuracy relative to a random model (AUC = 0.50). No Leopards existed historically at KY. Thus, no potential competitor was included in that model.

| Model | Factors included in the model | AUC |
|--------------------------|-----------------------------------------------------|------|
| <i>Neofelis nebulosa</i> | | |
| National | Elev (1.00), Prey (0.85), Habitat (0.61) | 80.2 |
| HKK | Habitat (1.00), Prey (0.47) | 75.5 |
| KY | Elev (1.00), Edge (0.77), Human (0.62), Rain (0.45) | 80.4 |
| <i>Panthera pardus</i> | | |
| National | Prey (1.0) | 85.0 |
| HKK | Prey (1.00), Tiger (0.64) | 62.1 |
| KK | Prey (1.00), Tiger (0.78) | 84.3 |
| <i>Panthera tigris</i> | | |
| National model | Prey (1.00), Habitat (0.92) | 79.9 |
| HKK | Water (1.00), Prey (0.59), Habitat (0.48) | 63.3 |
| KK | Rain (1.00), Prey (0.64) | 72.6 |
| KY | Human (1.00), Elev (0.91) | 83.2 |

biotic factors were included or not (Table S4). It should be noted, however, that areas with greater than average rainfall were positively associated with Clouded Leopard and Tiger presence in the abiotic models only, whereas *Habitat* was considered moderately important when biotic factors were included. Leopards showed a preference for low elevations and areas far from roads and villages in the abiotic only models. These models, however, generally had poor overall fit (Table S4).

The global model (before parameter selection) for each predator contained the seven habitat variables and *Prey*. The potential competitor was left out of the *national* models because combinations of potential competitors do not co-occur in all protected areas, potentially biasing the analysis. The addition of the selected habitat variables usually only marginally improved model fit over the models containing *Prey* only.

CLOUDED LEOPARD.—Clouded Leopard detection was most consistently associated with higher elevations and a high likelihood of prey presence (Table 3). Cameras that detected Clouded Leopards were on average 144 m higher in elevation than cameras that did not detect Clouded Leopards, although Clouded Leopards were photographed anywhere from 90 to 1253 m in elevation.

LEOPARD.—Unlike Clouded Leopards, where the models were somewhat idiosyncratic, the Leopard models were consistent. The *national model* and the two models for individual protected areas

all identified presence of potential prey as the primary correlate of Leopard detection (Table 3). Presence of tigers was negatively correlated with Leopard presence in both individual protected areas.

TIGER.—For tigers, *Prey* was the most important factor followed closely by *Habitat* (Table 3). *Habitat* showed a similar pattern in Tigers and Clouded Leopards; an association with mature evergreen forests at the national level, but a correlation with grasslands and more open areas within two individual protected areas (HKK and KK). Protected area complexes with potential for sustaining tiger populations in the long-term in Thailand are all >2000 km² (Lynam 2010). In these larger reserves tigers appear to prefer core areas where there is mature forest. In protected areas where there is a mosaic of closed evergreen forest and semi-open deciduous dipterocarp forest, tigers occur across this mosaic.

ASSOCIATIONS AMONG PREDATORS.—Nonparametric Spearman rank correlations of occurrence across 10 protected areas between Clouded Leopard and Leopard occurrence rates were -0.54 (NS), between Leopards and tigers of 0.12 (NS), and between Clouded Leopards and tigers of -0.03 (NS). The negative correlation between occurrence of Clouded Leopards and Leopards suggests a possible negative interaction between the two species, but the analysis is inconclusive, most likely due to small sample size and the consequent lack of statistical power. Occurrence rates of Clouded Leopards were not significantly higher in protected areas without leopards (or at least nondetected leopards) (mean 12.5%) than in those with leopards (9.0%) (one-tailed *t*-test: $t_{df=8, 0.05} = 0.42$, NS).

DISCUSSION

The major findings for this investigation are the following. (1) For the three largest felids in Thailand, the presence of certain prey species was generally the most important factor determining presence of the predator. Clouded Leopard and Leopard presence was associated with the presence of Red Muntjac and Eurasian Wild Pig. For Tiger, Gaur, Eurasian Wild Pig, and Sambar appeared to be the most important prey items. (2) Tigers do not exclude Leopards from habitats, but Leopards do appear to avoid tigers within their overlapping home ranges. (3) Some habitat features were associated with high probabilities of presence for Clouded Leopards and Tigers. Many of the habitat factors may be related to anthropogenic disturbances and threats. The evidence for this is particularly strong in Khao Yai. We elaborate on each of these points below.

PREY.—Presence of all three felids was strongly associated with certain prey species. Predator-prey relationships in this study are quite robust as they are consistent among and within protected areas, despite different models being used in each case to create the probability map for the prey species and despite favored prey items often having a preference for different habitat types. Care must be taken though, because the models do not show prefer-

ence, only what potential prey species carnivores are associated with and the strength of the association. The associations found in the models do not replace dietary studies for specific locations. Nevertheless, our results generally agree with known favored prey determined from diet studies.

Clouded Leopard presence was consistently associated with the presence of Red Muntjac and Eurasian Wild Pig. Little is known of the diet of Clouded Leopards in Thailand. The only study on the topic lists Brush-tailed Porcupine (*Atherurus macrourus*), Indochinese Ground Squirrel (*Menetes berdmorei*), Red Muntjac, Slow Loris (*Nycticebus coucang*), Hog Deer (*Axis porcinus*), and Sunda Pangolin (*Manis javanica*) as prey species (Grassman *et al.* 2005). Rabinowitz *et al.* (1987) list Sambar, Red Muntjac, Mouse Deer (*Tragulus javanicus*), Bearded Pig (*Sus barbatus*), Common Palm Civet (*Paradoxurus hermaphroditus*), various primates, and porcupine as prey in Borneo. Juvenile and adult Red Muntjac fall within the size prey that would be expected to be preferred by Clouded Leopards (*i.e.*, approximately their own body weight), and Choudhury (1993) witnessed Clouded Leopards stalking Eurasian Wild Pig. Clouded leopards are the most arboreal of the three predators we examined, and arboreal prey, such as primates likely constitute a greater proportion of their diet than tigers or leopards. Our analysis only considered terrestrial prey species and hence is less robust for clouded leopard than the other species; this may have contributed to the prey covariate falling second to an environmental covariate (elevation; see Table 3) in the national model for this species.

Detection of Leopard was consistently associated with the presence of Eurasian Wild Pig and Red Muntjac. Leopards in both Africa and Asia exhibit considerable flexibility in their diet, but appear to prefer prey between 20 and 75 kg (*e.g.*, Karanth & Sunquist 1995, Hayward *et al.* 2006), with juvenile and adult Eurasian Wild Pig fitting into this range. Rabinowitz (1989) suggested that leopards ate mostly Red Muntjac in Huai Kha Kaeng because Sambar, Gaur, and Banteng (*Bos javanicus*) are too large and Eurasian Wild Pig densities too low. Grassman (1999), using scat analysis, found Eurasian Wild Pig, Sambar, Red Muntjac, and Hog Badger contributed the most, respectively, in biomass to Leopard diets in Kaeng Krachan. In southern India, with habitat similar to much of Thailand, Karanth and Sunquist (1995) found that leopards ate Eurasian Wild Pig disproportionately little compared with other prey of a similar size, whereas Wegge *et al.* (2009) found that Eurasian Wild Pig was killed more often than expected, given their relative abundance in Nepal.

Consistent with the findings of studies across the region (*e.g.*, Karanth *et al.* 2004), Tiger presence was consistently associated with the presence of Gaur, Eurasian Wild Pig, and Sambar. Pet-dee (2000) and Prommakul (2003) both found Sambar, Gaur, and Banteng to be the most important prey items of Tiger in different parts of the Western Forest Complex of Thailand (which includes HKK and TY). We did not include Banteng in the models because of its highly restricted distribution and occurrence at low densities. While Gaur and Sambar were both strongly associated with Tiger presence, the species with the second strongest association was Eurasian Wild Pig. Eurasian Wild

Pig does not feature prominently in tigers diets in the Western Forest Complex (Petdee 2000, Prommakul 2003), but is known to be important elsewhere in Thailand (Steinmetz *et al.* 2010a) as well as in India, Nepal, the Russian Far East, and Sumatra (*e.g.*, Miquelle *et al.* 1996, O'Brien *et al.* 2003, Wegge *et al.* 2009).

Our results suggest that the two most commonly photographed potential prey species in the study areas, Red Muntjac and especially Eurasian Wild Pig, serve as the major prey species for the largest felids in Thailand. Eurasian Wild Pigs are heavily hunted in at least some parts of the region (Duckworth *et al.* 1999), but they also have a high reproductive capacity and recover quickly if protected from poaching (*e.g.*, Steinmetz *et al.* 2010b).

PREDATOR ASSOCIATIONS.—Intraguild interactions play a prominent role in shaping ecological communities and to limit population sizes of vertebrate predators (*e.g.*, Donadio & Buskirk 2006, Hunter & Caro 2008, Sergio & Hiraldo 2008, Ritchie & Johnson 2009). Of the two Clouded Leopard models at the level of individual protected areas, only Huai Kha Khaeng has Leopards. The model for HKK failed to find a relationship between detection of Leopards and Clouded Leopards. Thus, considering this regression model there is no evidence for Clouded Leopards avoiding Leopards. However, considering a larger scale, we observed a negative, but nonsignificant relationship between Clouded Leopard and Leopard occurrence across protected areas. We suggest interactions between Leopards and Clouded Leopards require further investigation.

In our study, there is no relationship between the occurrence of Leopards and Tigers at the site level. Logistic models for two protected areas, however, suggest that the detection of Leopards at these sites is negatively associated with the detection of Tigers at the scale of individual camera locations. While it has been shown that Leopards sometimes avoid tigers (Seidensticker *et al.* 1990, Odden *et al.* 2010), this behavior appears to depend strongly on the availability of both large and medium-sized prey, which mitigates interference competition between Tigers and Leopards (Karanth & Sunquist 1995). Avoidance also depends on habitat structure, particularly the presence of trees, which Leopards might use to escape from Tigers (Karanth & Nichols 1998). This agrees with our experience that Tigers and Leopards sometimes co-occur within protected areas in Thailand, frequently have overlapping home ranges, and even use the same roads and trails (Rabinowitz 1989). For example, the highest known densities of both Leopard and Tiger within Thailand are in the same area (Khao Nang Rum) within Huai Kha Khaeng (Simcharoen *et al.* 2008). It is notable that this site also has high densities of both medium (Red Muntjac, Eurasian Wild Pig) and large prey (Gaur, Banteng). The models suggest fine scale spatial avoidance, not displacement, of Leopards by Tigers from prime habitats.

The different outcomes for the logistic models and the occurrence analysis have biological explanations. Considered together, these models suggest fine scale spatial avoidance by leopards toward tigers within overlapping home ranges. Leopards are not displaced by Tigers from prime habitats, but rather avoid them at fine spatial (and perhaps temporal) scales. This interpretation corresponds to numerous field studies that have demon-

strated that subordinate (smaller) carnivore species often respond to potential interference competition and intraguild predation through active, fine scale spatial avoidance while inhabiting home ranges of larger species (Neale & Sacks 2001, Scognamillo *et al.* 2003, Steinmetz *et al.* 2011).

Another consideration is the effect of heavy hunting to which most protected areas have been subjected. All the protected areas we examined were subject to hunting to varying degrees. We could not quantify hunting pressure to model its effect on large cat distributions. Hunting pressure, however, did not appear to affect our results; large cats in protected areas that were relatively heavily hunted (Kaeng Krachan) were influenced by similar variables as cats in lightly hunted sites (Huai Kha Khaeng; Table 3). For example, leopard distributions in Huai Kha Khaeng and Kaeng Krachan were functions of the same set of abiotic and biotic variables (prey, and tiger distribution), and effect sizes of these variables were also similar (Table 3). Interspecific aggression is positively correlated with food stress in animals (*e.g.*, Polis *et al.* 1989, Palomares & Caro 1999). Most populations of large cats in Thailand can be considered food-stressed due to depletion of their prey base (Ngoprasert *et al.* 2007, Steinmetz *et al.* 2010b), and the size differential and morphology of tigers and leopards lends itself potentially to high levels of interference competition and interspecific killing (Donadio & Buskirk 2006). That Leopards did not appear to have their large-scale occurrence rates lowered by the presence of tigers, yet avoided them at smaller scales, maybe because Leopards and Tigers are forced to co-occur in the limited set of areas that support their preferred larger ungulate prey species.

ANTHROPOGENIC THREATS.—Khao Yai, which is surrounded by human-converted habitat, is a site with particularly high levels of disturbance (Albers & Grinspoon 1997). For Tigers, the distance to the nearest road or village and elevation both appear in the KY model but not the national model or any of the other models for individual protected areas. This is noteworthy as Tigers were present during the first surveys reported in this study, but apparently subsequently disappeared from Khao Yai (Lynam *et al.* 2006, Jenks *et al.* 2011). For Clouded Leopard, elevation, distance to forest edge, and distance to nearest road or village all appear in the model for Khao Yai. Only elevation, however, appears in any other model. Increased elevation and distance to the forest edge likely also reflect, at least in part, the reduced influence of poachers and human encroachment rather than habitat preferences. The central part of KY is mountainous and, due to the presence of the park headquarters and concentration of management activities, thought to be far less susceptible to poaching than other areas that are both easier to traverse and more accessible from roads and villages. It appears that the modeling process and the monitoring of the national park via trail-cameras have accurately captured the poaching pressure and ecological deterioration of large predator habitat during the course of a decade (Lynam *et al.* 2006, Jenks *et al.* 2011).

CONSERVATION IMPLICATIONS AND CONCLUSIONS.—The current study found that certain potential prey species were consistently

associated with the presence of the three largest felids in Thailand. Red Muntjac and Eurasian Wild Pig appear to be major prey items for Clouded Leopards and Leopards; whereas tigers were most closely associated with Gaur and Eurasian Wild Pig. Thus, recovery of populations or reintroduction success will likely be heavily dependent on conserving sufficient densities of ungulate prey. We also found evidence for negative associations among the three felids. The ecological relationships among the three predators requires further study and should be carefully considered when evaluating conservation approaches aimed primarily at increasing densities of one of the predators (Lynam 2010, Walston *et al.* 2010, Wikramanayake *et al.* 2011). Finally, this study demonstrates the value of collaboration among researchers in compiling larger camera-trap data sets that filter out some of the site-specific effects and allow the study of broader of ecological dependence and other conservation factors.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. Number of photographs of each species and number of camera-trap locations.

TABLE S2. Mean areas under the curve (AUC) for the receiver operating characteristic (ROC) and their 95% confidence intervals for the three felid species for each of the three models.

TABLE S3. The species included as prey in the predator models, the habitat variables included in each of the prey models, and the accuracy of the logistic regression model as measured by AUC.

TABLE S4. Abiotic variables and their relative importance values for Clouded Leopard (*Neofelis nebulosa*), Leopard (*Panthera pardus*), and Tiger (*Panthera tigris*).

FIGURE S1. Map of Thailand with each of the 13 protected areas where camera-trapping was conducted.

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