Environmental factors, human presence and prey interact to explain patterns of tiger presence in Eastern Thailand

E. Ash[1,2] (ID), Ż. Kaszta[1] (ID), A. Noochdumrong[3], T. Redford[2] (ID) & D. W. Macdonald[1] (ID)

1 Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, The Recanati-Kaplan Centre, Tubney House, Tubney, Oxon, UK
2 Freeland Foundation, Bangkok, Thailand
3 Ministry of Natural Resources and Environment, Bangkok, Thailand

Abstract

Thailand is one of the last strongholds for tigers *Panthera tigris* in mainland Southeast Asia. Evidence suggests heterogeneity in tiger presence in a globally important landscape in Eastern Thailand is potentially influenced by a complex interaction of prey, human presence and environmental conditions. Understanding these dynamics is of considerable importance for the conservation of tigers both in this landscape and elsewhere in their range. In this study, we examine which factors, among prey, human presence and environmental characteristics, best explain tiger presence in the Dong Phayayen–Khao Yai Forest Complex (DPKY). We collated survey data from 56,214 camera trap nights and evaluated the relationship between tiger presence and a suite of five prey, 11 human presence and eight environmental variables. We then used variance partitioning to discern the degree of variance in tiger presence explained by these factors. We documented strong, positive associations with wild boar *Sus scrofa* presence and prey richness, and strong, negative associations with human settlement density, public roads and presence of poachers. Environmental characteristics explained a greater relative proportion of variance (19.6%) in tiger presence than prey covariates alone (3.1%), particularly confounded with human presence (31.1%). This suggests that environmental variables, especially when accompanied by anthropogenic factors, could be used to model potential tiger occurrence where other data may be lacking. Our approach may be helpful in providing guidance for prioritizing habitat, evaluating the effect of human presence and identifying key prey to provide a foundation for tiger protection and recovery.

Introduction

Catastrophic population declines over the past century, driven by hunting, habitat loss and prey depletion, have pushed the tiger *Panthera tigris* precipitously close to extinction (Nowell & Jackson, 1996; Goodrich *et al*., 2015). In response, the species has been the focus of considerable funding, research and management efforts (Walston *et al*., 2010). Such investments appear to be generating positive results, such as recent announcements of a rise in global tiger numbers, though not without debate (Karanth *et al*., 2016; WWF, 2016*a*, 2016*b*; Harihar *et al*., 2017).

In contrast to recent cautious optimism, dramatic declines in tiger populations (Lynam & Nowell, 2011; Goodrich *et al*., 2015) and habitat (Joshi *et al*., 2016) in Southeast Asia cast doubt on the future of the Indochinese tiger *Panthera tigris corbetti*, one of the most poorly understood

subspecies. It is now possible that Cambodia, Lao PDR and Viet Nam have lost viable tiger populations (Lynam & Nowell, 2011; Gray *et al*., 2017; Rasphone *et al*., 2019). The potential loss of populations from these countries and continuing loss of habitat would represent a considerable challenge for meaningful recovery of tigers in the region.

These overall trends are evident in Thailand, one of the last remaining strongholds for tigers in Southeast Asia. While there are suggestions that the tiger population in Thailand is relatively low and has suffered national range restriction in recent years (Pisdamkam *et al*., 2010; DNP, 2016), long-term investments in law enforcement capacity may be providing a foundation for recovery in its largest source population (Duangchantrasiri *et al*., 2016). Further, a recent study in the Dong Phayayen–Khao Yai Forest Complex (DPKY) in eastern Thailand has established this understudied landscape as one of the few remaining breeding populations

known for the Indochinese subspecies (Ash *et al.*, 2020). DPKY has become a landscape of global conservation significance for tigers, underscoring the importance of improving scientific understanding of its population.

The landscape has been defined by considerable changes throughout its history which have played a major role in shaping the current state of wildlife conservation in the area. Over the past century, the interaction of environmental factors and anthropogenic activity have led to modification of habitat, such as conversion of lowland forests, and proliferation of roads and settlements, facilitating varying degrees of human presence (Rabinowitz, 1993; Lynam, Round, & Brockelman, 2006; Stokes, 2017). This complex history has had direct influence on tigers and the prey species which underpin their survival.

Given DPKY's history, the interaction of environmental, prey and human factors on recent tiger distribution is likely complex. In tiger studies elsewhere in their range, prey emerges as the strongest, or among the strongest, predictors of tiger presence (Karanth *et al.*, 2011; Harihar & Pandav, 2012; Ngoprasert *et al.*, 2012; Barber-Meyer *et al.*, 2013) with evidence suggesting an optimal tiger-prey body mass ratio of approximately 1:1 (~60–250 kg; Hayward *et al.*, 2012). Conversely, studies also report strong negative associations between tiger presence and anthropogenic disturbance, such as roads (Kerley *et al.*, 2002) and proximity to settlements (Sunarto *et al.*, 2012), though these relationships may not be ubiquitous (Carter *et al.*, 2012). Understanding the degree to which these factors broadly explain tiger presence on their own and are confounded could provide critical information for managers to develop protection strategies and inform additional, focused research.

At this critical juncture for tigers in Southeast Asia, understanding how tiger presence is affected by prey, threats and landscape characteristics is of considerable importance. Therefore, our goal in this study was to examine which factors, among prey, human and environmental characteristics, best explain the patterns of tiger presence in DPKY. To do so, we modelled several prey, human and landscape variables and compared the extent to which tiger occurrence is explained by these factors using variance partitioning. We tested three hypotheses in this study. First, we predict that tigers will have strong, positive associations with large-bodied (>175 kg) prey species. Second, tigers will have strong, negative associations with human habitation and, to a lesser degree, human presence. Third, we predict prey will better explain tiger presence compared to human or environmental characteristics, given the established importance of prey as a major limiting factor in tiger presence.

Materials and methods

Study area

The Dong Phayayen–Khao Yai Forest Complex (DPKY) spans 6155 km^2 in eastern Thailand and includes five protected areas (PAs): Khao Yai National Park (KYNP), Thap Lan National Park (TLNP), Pang Sida National Park (PSNP),

Ta Phraya National Park (TPNP) and Dong Yai Wildlife Sanctuary (DYWS; Fig. 1). Designated as a UNESCO World Heritage Site for its outstanding natural value, the complex is believed to host at least 112 mammal, 392 bird and 200 reptile/amphibian species (UNESCO, 2017), among them, the flagship Indochinese tiger. Ash *et al.*, (2020) identified six prey species potentially supporting the presence of tigers in DPKY: banteng *Bos javanicus*, gaur *Bos gaurus*, Northern red muntjac *Muntiacus vaginalis*, sambar *Rusa unicolor*, Chinese serow *Capricornis milneedwardsii* and wild boar *Sus scrofa*.

Potential sources of disturbance through human activities are diverse. DPKY is situated almost completely within a human-dominated matrix of villages, agriculture, silviculture and infrastructure. The complex supports a substantial tourism industry in some areas and major roads occur between KYNP-TLNP and TPNP-DYWS. Smaller roads also facilitate varying degrees of controlled and uncontrolled vehicle access into these PAs. Human incursions into DPKY include local collectors of non-timber forest products, wildlife poachers and illegal loggers. Law enforcement patrols by park rangers are conducted regularly.

Camera-trap surveys

Species presence data were collated from a non-invasive tiger camera-trap surveys from 2008 to 2017 (Fig. 1; see Ash *et al.*, 2020). Surveys were conducted opportunistically, varying in coverage and intensity. TLNP accounted for the highest proportion of survey effort (22 168 trap nights; 39% of total) with DYWS accounting for the least amount of survey effort (3427 trap nights; 6% of total). Survey effort generally increased as access to resources improved, covering all five PAs in the complex. Cameras were placed to maximize the detection of tigers by prioritizing camera placement in areas with previous tiger or prey records and identifying topographic or other features (e.g. roads, trails) likely used by tigers (Karanth & Chundawat, 2002; Sunarto *et al.*, 2012; Barber-Meyer *et al.*, 2013). Detections at one camera station were considered to be independent if they occurred after a 30-min period (O'Brien, Kinnaird, & Wibisono, 2003). This resulted in a total of 1166 tiger detections for analysis, as well as 10 726 detections of potential prey species and 21 910 human or human-related detections from 56 214 trap nights (Data S1; Table 1). A more comprehensive description of surveys is provided in Ash *et al.* (2020).

Variables

Based on information from previous studies on tigers throughout their range (Ngoprasert *et al.*, 2012; Sunarto *et al.*, 2012; Barber-Meyer *et al.*, 2013; Hebblewhite *et al.*, 2014), we assembled a suite of relevant predictor variables to explain variability in tiger detections in relation to prey and human presence (Data S1; Table 2). Presence was incorporated via photographic capture rate indices (PCRI) of four prey species as described by Ash *et al.*, (2020) – gaur, muntjac, sambar and wild boar. This was calculated as the
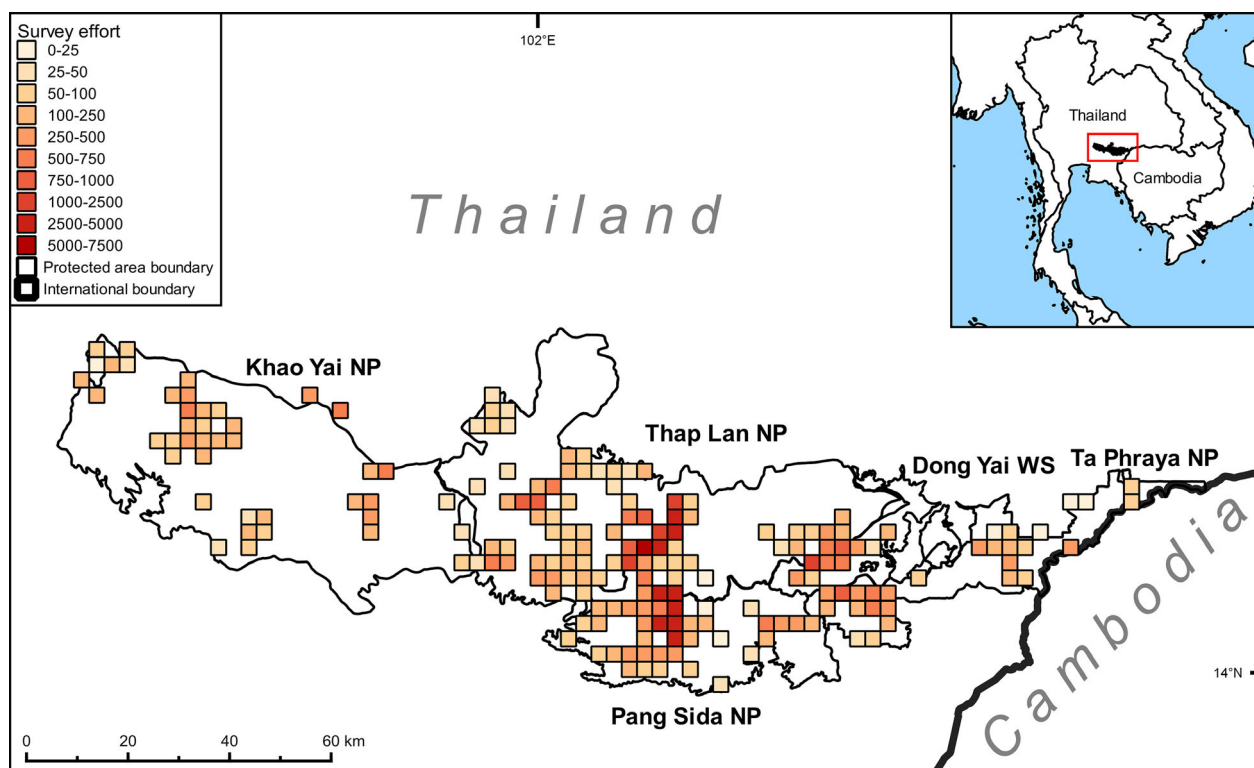
Figure 1 Map of the five protected areas within the Dong Phayayen–Khao Yai Forest Complex (DPKY; ~14°00′ to 14°33′N and ~101°05′ to 103°14′E; derived from Ash *et al.* (2020) – Dong Yai Wildlife Sanctuary (DYWS), Khao Yai National Park (KYNP), Pang Sida National Park (PSNP), Thap Lan National Park (TLNP) and Ta Phraya National Park (TPNP). Survey locations are represented by 3 × 3 km grids, shaded by total survey effort (total camera-trap nights; 2008–2017).

number of independent detections per 100 camera-trap nights. We included a prey richness covariate as the number of prey species detected for each station; this covariate also included the detection of banteng and serow, which were considered too rare to include as separate covariates. In this study, we define large prey as species with a mean body mass > 175 kg (sambar and gaur), medium-sized prey as species with a mean body mass from 20 to 175 kg (wild boar) and small prey species with a body mass < 20 kg (muntjac), designations similar to those in other tiger studies (Karanth & Sunquist, 1995; Karanth & Nichols, 1998; Andheria, Karanth, & Kumar, 2007; Steinmetz, Seuaturien, & Chutipong, 2013).

Human variables were determined based on direct human presence detected on camera traps and at broader scales. Among covariates related to human presence, we included PCRI for poachers (identified via weapons, equipment, carrying dead wildlife/timber etc.), domestic dogs, park rangers, vehicles and other humans (which include all humans and vehicles, except rangers and poachers). To evaluate broader scale human influence, we generated several GIS-based covariates at 30-m resolution to match the resolution of environmental variables from Ash *et al.* (In press). Using ArcGIS (ESRI, 2015), we calculated Euclidean distance to roads (Royal Forestry Department, 2000; GISTDA, 2005; 2018 Google, US Dept of State Geographer, Image Landsat/

Copernicus) for two classes: uncontrolled public roads, most of which occur just inside or outside the parks, and controlled private (park) roads, which are managed by parks to regulate access. We also calculated distance to park substation (Royal Forestry Department, 2000). To evaluate the potential influence of settlements, we calculated kernel density of settlements surrounding DPKY in ArcGIS (ESRI, 2015; 2018 Google, US Dept of State Geographer, Image Landsat/Copernicus). We also included the Global Human Influence Index dataset (WCS & CIESIN, 2005), summarizing population density, human land use and infrastructure, and human access.

In addition to prey and human covariates, we also included relevant environmental variables developed for the multiple-scale shape-optimized model in Ash *et al.* (In press). In this study, authors tested the effect of 47 environmental variables (Data S2; Table 1) on tiger occurrence based on the same camera-trap dataset (Ash *et al.*, 2020) at seven spatial scales (250 m to 16 km), derived from spatial statistics and including several landscape metrics (focal mean/percentage of landscape, standard deviation, correlation length, contrast-weighted edge density, patch density and aggregation index), generated by moving windows of size corresponding to each scale. The authors also tested variables transformed by five different functional shapes (linear, quadratic, log, exponential and negative exponential). Variables

were evaluated at each scale and functional form in univariate models with tiger presence as the response variable, with optimal scale and functional form determined by AICc. Following filtering of variables based on $P > 0.05$ and Pearson's correlation, remaining variables were included in a fully averaged multivariate model with performance evaluated via area under the relative operating characteristic (ROC) curve (AUC). The model, which performed exceptionally well (AUC 0.93), included eight variables: percentage of secondary forest (log, 16 km), correlation length of secondary forest (linear, 4000 m), camera effort, percentage of bamboo forest (linear/quadratic; 16 km), standard deviation of elevation (linear/quadratic, 16 km), focal mean of terrain roughness index (linear/quadratic 16 km), percentage of open forest (linear, 16 km) and correlation length of reforested areas (linear/quadratic, 8 km). Environmental factors in our study were defined by the same set of variables and their coefficients as in Ash *et al*. (In press) at their appropriate spatial scales and functional forms (Table 2c; see Data S2).

Tiger occurrence models

To evaluate the within-group effect of each covariate on tiger detections, we developed generalized linear models (GLM) for each of the three factors (prey, human and environment). The models included binomial tiger detection data as the response variable, covariate data as the explanatory variable and survey effort (CTN) as a fixed effect, with binomial distribution using a logit link function. To eliminate within-group collinearity and maintain collinearity across the groups for variance partitioning analysis, we conducted a Pearson's correlation test between variables in each category (prey and human) with correlation threshold of $|r| > 0.6$, removing variables of higher AICc value via univariate regression (Burnham and Anderson 2002). The best combination of remaining covariates in each group were determined by subsetting best performing GLMs in 'BIOSTATS' (McGarigal, 2018), ranked by ΔAICc (defined in our model as ΔAICc < 2), ranking variable importance in final models and generating averaged coefficients based on Akaike's model weight (w_i). These steps were also carried out for the environmental model generated by Ash *et al*. (In press).

To evaluate model performance, we calculated and compared statistics indicating model discriminatory ability. Specifically, we evaluated sensitivity, specificity, percent correctly classified (PCC), kappa and AUC. Second, we tested the influence of each covariate on probability of tiger presence by calculating the difference observed when the covariate increases from the 10th to 100th percentile, using standardized values while holding other covariates at their medians. Covariates were transformed to non-standardized values and plotted to evaluate changes in probability of tiger presence relative to changes in covariate values.

Variance partitioning

We used all final variables in each group (five prey, 11 human and eight environmental variables) to conduct variance partitioning analysis (Borcard, Legendre, & Drapeau, 1992), in order to quantify the extent to which prey, human and environmental factors account for variation in tiger detections across DPKY. Variance partitioning has been used in a number of ecological modelling studies (Cushman & McGarigal, 2004; Bhattarai & Kindlmann, 2013; Timm *et al*., 2016) and is useful in discerning the explanatory power of independent and confounded models on a shared response.

Variance partitioning was conducted using the function *varpart* within the package 'vegan' in R (R Development Core Team, 2017; Oksanen *et al*., 2018), including the three described types of covariates (prey, human and environmental) with camera effort as a fourth explanatory component and binomial tiger detections as the response.

Results

Among an original 11 covariates for human presence and five covariates for prey, four human presence covariates were dropped (domestic dog, other humans, distance to park substation and distance to all roads) and one prey covariate was dropped (muntjac) due to $P > 0.05$. Pearson's correlation test for variables within the two groups did not indicate correlation ($|r| > 0.6$) between remaining covariates.

Overall model performance was strong for all groups of covariates (AUC > 0.80; Table 1). The environmental model from Ash *et al*. (In press) exhibited the strongest performance by AUC (0.93), followed by human factors (0.90) and prey (0.80). For other model performance statistics, human factors outperformed others in percent observations correctly classified (PCC) and specificity with the environmental model performing better based on sensitivity. Further, Kappa for human factors (0.65) was similar to the environmental model (0.65), but notably higher than that of prey (0.41), demonstrating exceptional ability to correctly discriminate between detection and non-detection points. All groups had relatively high specificity values – 0.96 for human factors, 0.93 for environment and 0.86 for prey – indicating a strong ability to predict non-detection points.

Prey model

All four prey covariates were included in the fully averaged model (Table 2a) together with camera effort. AIC variable importance was highest for wild boar, prey richness and camera effort, both present in $n = 3$ model subsets, and lowest for sambar and gaur ($n = 1$).

Table 1 A summary of performance statistics for prey, human and environmental models, the latter derived from Ash et al. (In press)

Model	Max Kappa Cut-point	PCC	Sensitivity	Specificity	Kappa	AUC
Prey	0.2700	0.7954	0.5526	0.8631	0.4092	0.80
Human	0.4700	0.8891	0.6491	0.9560	0.6504	0.90
Env.	0.4300	0.8815	0.7018	0.9315	0.6455	0.93

Table 2 Fully averaged model results for (a) human presence, (b) prey and (c) the environmental model (Ash et al, In press) including standardized regression coefficients (β), standard error (SE), adjusted standard error (Adjusted SE), z-value (z), significance (p), AIC variable importance (AIC Var. Imp) and change in probability with increasing variable values from 10th to 100th percentile (Δprob). Vehicle, poacher, wild boar, sambar and gaur covariates were derived from photographic capture-rate index values (PCRI; detections per 100 camera-trap nights). The environmental model includes optimal scale and functional form (^{L}linear, ^{Q}Quadratic, ^{LOG}Logarithmic)

	β	Adjusted SE	z	P	AIC Var. Imp	Δprob
(a)						
(Intercept)	−1.459	0.133	10.984	<0.001	—	—
Wild Boar	0.297	0.111	2.674	0.008	3	0.51
Prey Richness	0.442	0.167	2.647	0.008	3	0.24
Camera effort	0.990	0.241	4.108	<0.001	3	0.87
Sambar	0.104	0.119	0.872	0.383	1	0.33
Gaur	−0.074	0.132	0.556	0.578	1	−0.07
(b)						
(Intercept)	−2.349	0.268	8.775	<0.001	—	—
Vehicle	0.286	0.154	1.860	0.063	2	0.75
Distance to public road	1.005	0.197	5.112	<0.001	3	0.67
Distance to park road	−0.355	0.182	1.955	0.051	2	−0.11
Settlement density	−1.614	0.485	3.327	0.001	3	−0.19
Camera effort	1.426	0.270	5.287	<0.001	3	0.91
Poacher	−0.678	0.517	1.313	0.189	1	−0.12
(c)						
(Intercept)	−1.367	0.314	4.352	<0.001	—	—
% Secondary forest (16 km)^{LOG}	−0.777	0.210	3.702	<0.001	2	−0.23
Correlation length secondary forest (4 km)^L	−0.701	0.235	2.978	0.003	3	−0.13
Camera effort (# trap nights)	1.460	0.309	4.718	<0.001	3	0.92
% Bamboo (16 km)^L	1.028	0.525	1.960	0.050	2	0.55
DEM standard deviation (16 km)^L	0.995	0.308	3.226	0.001	1	0.13
% Bamboo (16 km)^Q	−0.072	0.232	0.309	0.757	2	0.55
DEM standard deviation (16 km)^Q	−0.866	0.336	2.575	0.010	1	0.13
Focal mean of terrain roughness index (16 km)^L	1.165	0.502	2.317	0.020	2	0.13
Focal mean of terrain roughness index (16 km)^Q	−1.671	0.579	2.887	0.004	2	0.13
% Open forest (16 km)^L	−2.353	0.457	5.149	<0.001	1	−0.58
Correlation length of reforested areas (8 km)^L	0.968	0.321	3.011	0.003	1	0.17
Correlation length of reforested areas (8 km)^Q	−0.555	0.195	2.844	0.004	1	0.17

Variable importance, as determined by standardized coefficients, was highest for camera effort ($\beta = 0.990 \pm 0.241$), followed by prey richness ($\beta = 0.442 \pm 0.167$) and wild boar ($\beta = 0.297 \pm 0.111$). Both gaur ($\beta = -0.074 \pm 0.132$) and sambar ($\beta = -0.104 \pm 0.119$) had adjusted standard errors crossing zero.

Predicted tiger presence had a strong, positive association with camera effort, with a change (Δ) of 0.87 as camera effort values increased from 10th to 100th percentiles. Wild boar appeared to be a strong predictor of tiger presence, with predicted probability increasing from 0.14 to 0.65 (Δ0.51) as PCRI values increased to 0–58 detections per 100 CTN. There was a moderate increase in predicted probability in tiger presence from 0.15 to 0.48 (Δ0.33) as sambar PCRI increased from 0 to extreme values at the 100th percentile (288 detections/100 trap nights). The presence of gaur appeared to have a marginally negative influence on predicted tiger presence, with predicted probabilities declining from 0.15 to 0.08 (Δ-0.07) as PCRI increased from 0 to 28. However, these relationships for gaur and sambar are uncertain given adjusted SE for their standardized coefficients cross zero. Predicted tiger presence was also positively associated with overall prey species richness, increasing from 0.08 to 0.32 (Δ0.24) as richness increased from 0 to 5 prey species detected.

Human model

A total of six human covariates were included in the fully averaged model (Table 2b) – vehicles, camera effort, distance to park roads, distance to public roads, poacher PCRI and settlement density.

AIC variable importance varied marginally across covariates with highest values for camera effort, distance to public roads and settlement density ($n = 3$), followed by vehicles, and distance to park roads ($n = 2$) and poacher presence ($n = 1$). Influential covariates positively associated with tiger presence, as determined by standardized coefficients, included camera effort ($\beta = 1.426 \pm 0.270$) and distance to public roads ($\beta = 1.005 \pm 0.197$). Conversely, covariates

with a notably strong negative association included settlement density ($\beta = -1.614 \pm 0.485$) and, to a lesser degree, poacher PCRI ($\beta = -0.678 \pm 0.517$).

Predicted tiger presence relative to changing covariate values was positively associated with camera effort ($\Delta 0.91$) and vehicles ($\Delta 0.75$). Tigers were also positively associated with distance to public roads with probabilities increasing from 0.04 to 0.71 ($\Delta 0.67$) as distance to public roads increased from 570 m to over 17 400 m. Changes in predicted tiger presence was less pronounced in cases where tigers were negatively associated with covariates. Predicted tiger presence with increasing settlement density decreased from 0.19 to 0 (Δ-0.19) as density increased from almost 0 to 0.13. Predicted tiger presence steeply declined from 0.12 to almost 0 (Δ-0.12) as poacher PCRI increased from 0 to 100 detections per 100 trap nights. Similarly, as distance to park roads increased from less than 100 m to over 27 000 m, we observed a moderate decline in predicted tiger presence from 0.14 to 0.03 (Δ-0.11).

Environmental model

As discussed in Ash *et al.*, (In press), the environmental model (Table 2c) describes positive associations between tigers and percentage of bamboo forest ($\beta = 1.028 \pm 0.525$), moderate topographic heterogeneity (standard deviation of elevation [$\beta = 0.995 \pm 0.308$] and focal mean of terrain roughness index [$\beta = 1.165 \pm 0.502$]) and reforested areas

($\beta = 0.968 \pm 0.321$), and negative associations with secondary ($\beta = -0.777 \pm 0.210$) and open forest ($\beta = -2.353 \pm 0.457$). Additional information on changes in predicted tiger presence as variables increase from 10th to 100th percentiles can be found in Table 2c and Data S2.

Variance partitioning

The relative proportion of variance explained among the three main groups of variables (prey, human and environment), and camera effort varied considerably with a high degree of collinearity (Fig. 2). Environmental factors, independent and confounded with others, accounted for 81.6% of the relative proportion of variance explained, followed by 59.3% for human factors, 36.7% for camera effort and 33.2% for prey. However, the relative proportion of variance explained exclusively by independent factors was highest for environment (19.6%), followed by camera effort (5.2%), prey (3.1%) and human presence (2.1%). Environmental and human factors jointly explained 31.1% of relative proportion of variance, the highest among confounded factors (Data S1; Table 3). Relative proportion of variance explained jointly for environment, prey and human factors was 7.3%.

Discussion

We evaluated the degree to which prey, human and environmental characteristics explain tiger presence in the Dong
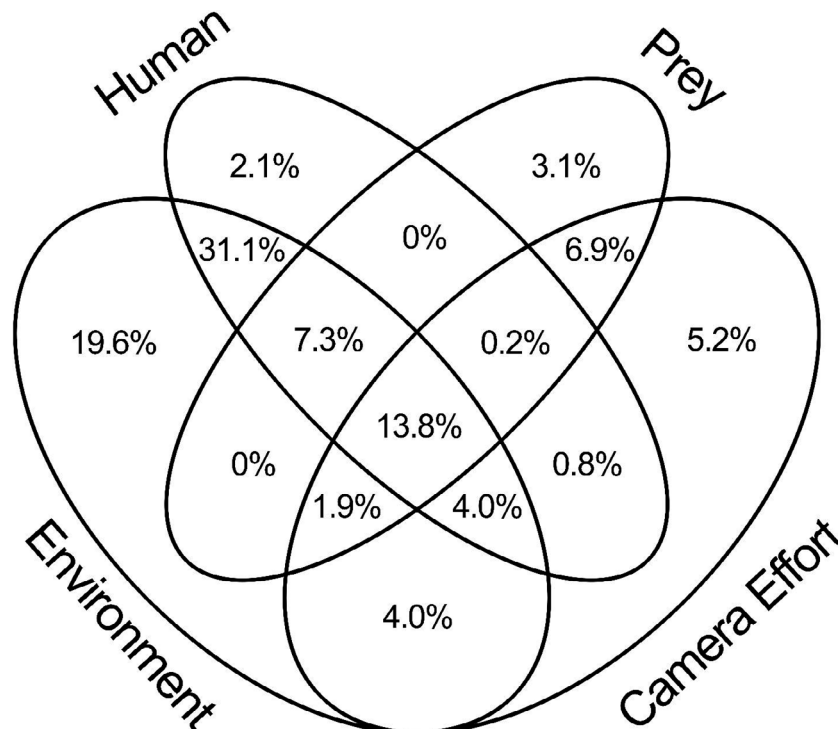

Figure 2 Relative proportion of variance in tiger detections explained by environmental, human and prey factors and camera effort. Confounded factors (areas of overlap) describe variance which cannot be explained by a single model.

Phayayen–Khao Yai Forest Complex, a tiger landscape of global conservation priority. Environmental variables, particularly confounded with human factors, explained a greater proportion of variance in tiger presence than any other factor in our study, potentially due to environmental covariates more comprehensively accounting for factors influencing tiger presence, including presence of prey and human access, than either of these factors independently. Importantly, we documented strong associations with medium-sized prey (wild boar) and areas of high prey richness while also documenting strong negative associations with anthropogenic factors, particularly settlement density, public roads and increased poaching presence.

Our first hypothesis predicted that tigers would have strong, positive associations with large-bodied (>175 kg) prey species, in particular, sambar and gaur. The presence of prey species is a critical factor in the presence and persistence of tigers (Karanth & Stith, 1999; Karanth *et al*., 2004) and a number of studies throughout the tiger's range indicate a preference for large prey (Karanth & Sunquist, 1995; Biswas & Sankar, 2002; Bagchi, Goyal, & Sankar, 2003). Our results do not support this hypothesis. In our study, tiger presence had strong, positive associations with wild boar, considered in our study a medium-sized species, while positive or negative relationships could not be determined for sambar and gaur, the two largest prey species evaluated. Wild boar are relatively widespread in the complex compared to sambar (Ash *et al*., 2020) and differences in availability of these prey species across the complex may have been a factor in the strength of variable coefficients for these species. These results are partially consistent with other studies in Thailand. In Ngoprasert *et al*. (2012), tigers had strong overall associations with wild boar; however, in contrast to our results, gaur was considered to have the highest importance in both national and Khao Yai NP models and tiger presence was also positively associated with sambar. In Western Thailand, studies have suggested wild boar (Steinmetz *et al*., 2013), gaur, sambar and banteng to be important prey species (Petdee, 2000; Prommakul, 2003). Wild boar and deer species, such as sambar, are suggested to be important prey species elsewhere in the tiger's range (Sunquist, Karanth, & Sunquist, 1999; Biswas & Sankar, 2002; Hayward, Jedrzejewski, & Jedrzewska, 2012; Petrunenko *et al*., 2016), in some cases, more so compared to gaur and muntjac (Sunquist *et al*., 1999; Biswas & Sankar, 2002). Hayward *et al*. (2012) suggest tigers optimally select prey with a similar body mass, corresponding roughly to large cervids (e.g. sambar) and wild boar which we considered 'large' and 'medium' prey species, respectively. In future studies testing similar hypotheses, prey size classifications may be more appropriate relative to tiger body mass (e.g. wild boar and sambar as 'optimally sized' prey).

In addition to strong positive associations with wild boar, we also documented relatively strong positive associations with overall prey richness. Availability of diverse prey of different size classes is thought to be an important factor in the persistence of large felids (Sandom *et al*., 2017) and, more broadly, richness and persistence of large carnivores

may be underpinned by the richness of prey species (Sandom *et al*., 2013). It is possible that prey species richness, in addition to specific prey species, augments tiger presence in certain areas in DPKY.

In our second hypothesis, we predicted that tigers would have strong, negative associations with human habitation and, to a lesser degree, human presence. Our results are consistent with this hypothesis. Tiger presence in our study had strong, negative associations with public roads and settlement density, and relatively strong negative associations with the presence of poachers. These results are consistent with evidence in other studies suggesting broad negative associations with human activity overall (Karanth *et al*., 2011; Harihar & Pandav, 2012; Ngoprasert *et al*., 2012; Barber-Meyer *et al*., 2013). More specifically, strong negative associations with settlements and public roads is supported by studies elsewhere in the tigers range (Kerley *et al*., 2002; Linkie *et al*., 2006; Sunarto *et al*., 2012). The negative association with the presence of poachers is also consistent with studies highlighting the potentially catastrophic impacts of poaching on tiger and prey populations, even in seemingly intact forest (Kenney *et al*., 1995; Chapron *et al*., 2008; Steinmetz *et al*., 2010). Negative associations with human settlements, public roads and poaching presence appears to be almost universal across the tiger's range (Kerley *et al*., 2002; Kanagaraj *et al*., 2011; Hebblewhite *et al*., 2012; Sunarto *et al*., 2012; Barber-Meyer *et al*., 2013), part of a broader trend of these factors being associated with declines of large carnivores globally (Ripple *et al*., 2014; Wolf & Ripple, 2017). Our results suggest these factors are a major influence in tiger distribution in DPKY.

Our results depart somewhat from our second hypothesis with positive associations with park roads and vehicles. In our study, we distinguished between public roads, primarily occurring outside park boundaries, and park roads maintained by PAs which facilitate access for patrolling and, in some areas, tourism. Our study is distinguished in this regard from studies reviewing effects of public roads of varying intensity of use or navigability rather than uncontrolled versus controlled access (Kerley *et al*., 2002). Positive associations with park roads in our study are likely a result of tigers using certain roads for efficient travel through the landscape (Kerley *et al*., 2002; Sunquist, 2010; Carter *et al*., 2012). Further, many of the vehicles documented in this study were vehicles used by PA staff for patrolling which may overlap with areas of protection priority, such as areas that support the presence of tigers. Elsewhere in Thailand, a study by Ngoprasert *et al*. (2007) did not document significant differences in detection rates of leopard among different categories of vehicle traffic rates. The authors speculate this may be due to temporal separation, a factor in patterns of co-occurrence in Carter *et al*. (2012). This may have also been a factor in our study. Regular use of roads by felids and other species have been documented in other studies (Di Bitetti *et al*., 2010; Di Bitetti, Paviolo, & De Angelo, 2014). However, the relationship between these species and roads is likely complex. Due to the study design, we were unable to evaluate fine-scale effects of vehicle presence on tigers. Thus,

associations with vehicles do not necessarily imply tolerance or the absence of negative influence.

Our third hypothesis was that prey itself would better explain tiger presence compared to human presence or environmental characteristics, given the established importance of prey as a major limiting factor in tiger presence (Karanth & Stith, 1999; Karanth *et al.*, 2004) and high importance of prey in other modelling studies (Kanagaraj *et al.*, 2011; Karanth *et al.*, 2011; Barber-Meyer *et al.*, 2013; Steinmetz, Seuaturien, & Chutipong, 2013). This hypothesis was not supported by our results. Independently, tigers had strong positive associations with prey and a lack of prey would certainly preclude tiger presence. However, contrary to our hypothesis, in terms of relative variance explained, variance partitioning indicated that prey alone explained less variance (3.1%) compared to other factors. In contrast to our predictions, environmental factors explained the greatest overall proportion of variance (19.6%), particularly confounded with human factors (31.1%).

Variance partitioning in our study indicated that tiger relationships with prey, in some cases, could be explained by a combination of environmental and human factors. Ash et al. (In press) described strong positive associations with habitat suitable for important prey species described in our study, strong positive associations with core habitat away from human habituation and strong negative associations with habitat near settlements that were heavily impacted by human activity. In effect, environmental covariates, including habitat, terrain and proxies of human and prey effects, may have been a more comprehensive predictor of tiger presence overall than prey or human factors on their own, resulting in higher explanatory performance. Specifically, it is possible that environmental covariates better accounted for important limiting factors for the presence of prey, including human presence, resulting in a high degree of collinearity. Importantly, this suggests that in some cases an environmental model, especially coupled with anthropogenic factors, could be used to model tiger occurrence where other data may be lacking. However, this approach would merit a high degree of caution since, regardless of environmental characteristics, poaching and prey depletion can eradicate tigers and other species from otherwise intact habitat (Benítez-López *et al.*, 2019). Application of this approach may be beneficial in poorly understood areas by identifying factors of notable influence on tiger presence to guide more specific and robust scientific enquiry. Rigorous studies to assess prey abundance and human pressure should be employed wherever possible to more comprehensively understand the influence of these factors on tiger presence.

Human presence explained a relatively large amount of variance in our study, and the effects of its variables on tiger presence were particularly strong. This relationship between human and environmental factors is evident in the high relative proportion of variance explained by confounded human and environmental factors. In DPKY, mountainous habitat has been the least prone to disturbance historically, with landscape characteristics limiting patterns of human influence. Overall, tiger presence in DPKY may be explained in

broad terms by the fact that little alternative habitat remains outside of more central areas and that variance in tiger presence is explained by differences in broad-scale environmental conditions, available habitat for prey, and refugia in which prey are subject to lower poaching pressure.

While our study reveals important associations with certain prey species, these associations should be distinguished from prey selection, which was outside the scope of this study and would require methods of diet analysis (Karanth & Nichols, 1998; Andheria, Karanth, & Kumar, 2007). Further, we did not include smaller potential prey species (<20 kg) given the presence of several larger prey species in our study area and strong representation of larger prey as being critically important in studies throughout the tigers range (Karanth & Sunquist, 1995; Biswas & Sankar, 2002; Bagchi, Goyal, & Sankar, 2003). Such species were not included in Ngoprasert *et al.* (2012) in modelling tiger associations with prey elsewhere in Thailand. Study design precluded adherence to key assumptions of occupancy modelling (Harmsen *et al.*, 2010; Welsh, Lindenmayer, & Donnelly, 2013), particularly those pertaining to independence and population closure necessary for calculating reliable estimates of detection probability. Thus, prey covariates were developed using detection rates (PCRI) as a surrogate to evaluate the influence of prey presence. We recommend future studies strive to incorporate data from studies explicitly designed for occupancy or capture-recapture frameworks where possible. Further, given spatial overlap of human presence with tiger and prey species, additional studies exploring the potential risk from disease transmission, such as from canine distemper virus (CDV; Seimon *et al.*, 2013) or African swine fever (Guberti *et al.*, 2019) may be warranted.

Implications for conservation

Our study suggests explanatory factors for tiger presence in the Dong Phayayen–Khao Yai Forest Complex are more nuanced than initially hypothesized. We documented strong, positive associations with wild boar *(Sus scrofa)* and prey richness, and strong, negative associations with human settlements, public roads and poachers. However, environmental characteristics, particularly confounded with human presence, explained a greater relative proportion of variance in tiger presence than prey covariates. Given the patterns of tiger presence in our study and consistent with studies from elsewhere in the tigers' range, we recommend prioritizing protection of key habitat, minimizing human presence and securing prey rich areas as part of ongoing tiger protection strategies in DPKY. We echo the sentiment of Kanagaraj *et al.* (2011) that, although these seemingly intuitive results, such as negative associations with anthropogenic factors, are not new, these are nonetheless important to quantify. Negative impacts of human influence have been documented broadly (Crooks, 2002; Foley *et al.*, 2005; Coffin, 2007), as well as more specifically for other large, wide-ranging species such as wolves (Lesmerises, Dussault, & St-Laurent, 2012) and bears (Linke *et al.*, 2013). However, the relationship between the presence of these species and

anthropogenic factors may be more complex than broader trends suggest (Hebblewhite & Merrill, 2008; Martin *et al.*, 2010; Carter *et al.*, 2012). Understanding the potential influence of human presence on tigers, particularly in concert with other factors such as prey or environmental factors, is particularly important for our study area for which landscape-scale assessments on tigers have been lacking.

Controlling poaching of prey, particularly wild boar, and minimizing disturbance to habitat will be crucial for tiger protection while restoration of degraded habitat and prey populations will improve prospects for long-term recovery of tigers in this landscape. Reducing infrastructure development that may otherwise fragment habitat or facilitate access, such as roads or dams, maintaining careful regulation of access into this landscape and additional research on potential finer-scale effects of vehicles on tiger presence is also warranted. Efforts are underway to mitigate the effects of one major roadway (UNESCO, 2017) though the extent to which this will facilitate tiger movement is not yet known. Understanding the degree to which tigers can move within and beyond this landscape, particularly in areas of higher human influence, will be critical to the development of long-term, broad-scale recovery strategies. We believe this study will be beneficial in guiding such strategies in DPKY, specifically within the realm of protection of prey and mitigation of potentially adverse human activity. Our approach may be helpful in other areas for providing guidance on prioritizing habitat, evaluating the effect of human presence and identifying key prey to provide a foundation for species protection and recovery.

Acknowledgements

Conflict of Interest

None.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Supplementary tables and figures.
Data S2. Environmental model summary.