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Dry-season habitat occupancy by ungulate tiger prey in the Hukaung Valley of northern Myanmar

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Abstract: We assessed habitat occupancy and distribution of principal tiger (*Panthera tigris*) ungulate prey species to assess factors affecting their occurrence and their potential contribution to low tiger presence in the core part of the Hukaung Valley Wildlife Sanctuary, in northern Myanmar. We surveyed for signs on 1,651 km of transects partitioned into 554 sampling units between November 2007 and May 2008. By incorporating seven environmental and four social covariates, we predicted habitat occupancy rates of 0.76 for gaur (*Bos gaurus*), 0.91 for sambar (*Rusa unicolor*), 0.57 for wild pigs (*Sus scrofa*), and 0.89 for northern red muntjac (*Muntiacus vaginalis*). Overall, shorter Euclidean distances to ranger stations and trails, decreased stream density, and broadleaved evergreen/semi-deciduous forest and relatively rare rain-fed cropland habitat occurrence positively influenced prey habitat occupancy; conversely, shorter Euclidean distances to villages, roads, and streams, higher elevations, and occurrence of mixed broadleaved and needle-leaved forest habitat negatively influenced occupancy. In addition, Euclidean distance to ranger stations, trails, and roads positively affected species detections, whereas shorter Euclidean distance to villages and streams, high elevations, and high precipitation negatively affected detections. Results indicated that all four prey species were relatively well-distributed through the Sanctuary core area, but comparisons with indices of abundance elsewhere suggest that prey density was low and would not likely support many tigers.

Key words: *Bos gaurus*, distribution, gaur, muntjac, *Muntiacus vaginalis*, *Panthera tigris*, *Rusa unicolor*, sambar, *Sus scrofa*, tiger, wild pigs.

Introduction

About 22% of mammal species worldwide are globally threatened or extinct in the wild due to habitat loss, utilization, and invasive species, and about 15% have insufficient data to assess their conservation status (Vié et al. 2009). Tiger populations (*Panthera tigris* Linnaeus, 1758), for example, have decreased dramatically from 100,000 in the last century to 3,200

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today while also suffering a contraction of their historical range by the synergetic effects of habitat loss (about 93%; Dinerstein et al. 2006), prey depletion, and direct hunting (Karanth et al. 2004; Walston et al. 2010; Barber-Meyer et al. 2013). Biologically, tigers cannot survive without adequate prey, even though habitats seem well protected. Ungulate prey, the important determining factor of tiger population density (Karanth and Stith 1999), is also decreasing because of habitat loss and fragmentation by agricultural expansion, road construction, and mining, and increased consumption (e.g., poaching) due to human population growth (e.g., Johnson et al. 2006; Steinmetz et al. 2010).

There are many ways to assess population abundance, but often they are difficult to employ. For example, mark-recapture methods are impractical to apply in some protected landscapes due to expense, time, and imperfect detection. Direct counting using line transect surveys (Buckland et al. 2001) is not always applicable due to the low density of target species and habitat composition. In the Hukaung Valley of Myanmar, for example, dense vegetation like rattan and bamboo brakes and other logistical constraints that limit the visual sighting of species is a problem. Therefore, useful methods are those that are reliable and cost-effective in producing reliable data needed for conservation. In some situations, indirect counting or sign surveys, along with occupancy modeling (Linkie et al. 2006; Hines et al. 2010; Karanth et al. 2011), is a practical approach, particularly for large-scale assessments.

Tiger occupancy is primarily influenced by the abundance of large prey species (Barber-Meyer et al. 2013; Duangchantrasiri et al. 2019). Therefore, we used extensive sign surveys to estimate the distribution and habitat occupancy of principal tiger prey species (gaur *Bos gaurus* (C. H. Smith, 1827), sambar *Rusa unicolor* (Kerr, 1792), northern red muntjac *Muntiacus vaginalis* (Boddaert, 1785), and wild pig *Sus scrofa* Linnaeus, 1758) in the Hukaung Valley Wildlife Sanctuary (HVWS) in northern Myanmar, an area where tiger density seemed low, and to assess potential tiger density (Karanth et al. 2004) (*Appendix 1-4*).

Study area

The Hukaung Valley, surrounded by deep jungle and steep mountain ranges to the north, west, and east, contains Myanmar's largest expanse of tiger habitat, covering approximately 17,373 km^2 in the country's northernmost state (~25º23´-27º23´N and 95º33´-97º18´E; Figure 1). The site ranges in elevation from 94 to 3,440 m and contains the watershed for the upper Chindwin River which joins the mighty Irrawaddy River. The plains contain a mosaic of broadleaf forest and grassland, the hill slopes are covered with broadleaf forest, and the mountains consist of temperate broadleaf forest, coniferous forest, and shrubland (Lynam et al. 2009). The study area is in the humid subtropical climate zone, having a mean annual rainfall of approximately 2,340 mm, and mean annual minimum and maximum temperatures of 18.8°C and 30.0°C, respectively. Myanmar's climate is greatly influenced by monsoons which help define three distinct seasons. The summer season runs from mid-February to mid-May, the rainy season from mid-May to mid-October, and the winter season from mid-October to mid-February.

This study was conducted in the core area (~1,800 km^2) located in the middle HVWS (Figure 1). There is now no human settlement within this area except along the southern edge on the Ledo Road, built by the alliance during World War II and which serves as the single major transportation route for the community. Local people also use footpaths along ridges and rivers to commute to their remote villages. There is no other man-made road except the Ledo. Waterways are the second major transportation option.

Historically, the local people in the Hukaung Valley were primarily Kachin, Shan, Naga, and Lisu tribes, indigenous people who rely mainly on shifting cultivation, non-wood forest product collection, and subsistence hunting. In establishing the HVWS, the government recognized the existence of indigenous people because of the value of existing biological and cultural diversity and to avoid undesirable issues for park management. However, compared to other protected areas in Myanmar, the local population growth in the HVWS is relatively low.

Materials and methods

An occupancy survey was carried out in the management-focused area of HVWS to establish a robust biological monitoring system to inform Hukaung Valley management decisions concerning tiger and prey conservation. In conducting the survey, a modified cluster sampling design was used (Hines et al. 2010) and followed Tigers Forever protocols (Karanth et al. 2008, 2011; cf. Vongkhamheng et al. 2013). The Hukaung Valley landscape was divided into 92 large blocks, each ~300 km² in size, to ensure encompassing the area of the largest home range of an adult male tiger. Among them, 6 blocks fell in the core area (~1,800 km²). Each block included 25 smaller sub-blocks (~13 km²), and then each of these was divided into four equal grid cells (~3.25 km²) (Figure 2). Within each grid cell, there were nine sampling destination points evenly spaced 600 m apart. The guideline for the survey specified that each team had to pass through at least five destination points, including the middle point. This survey design used 300 m of the survey line as a spatial replicate (Figure 3). The survey team recorded presence and absence data based on fresh tracks, pellets, and direct sightings of target species. However, in this study, only fresh footprints were used as presence-absence data for data consistency and data freshness.

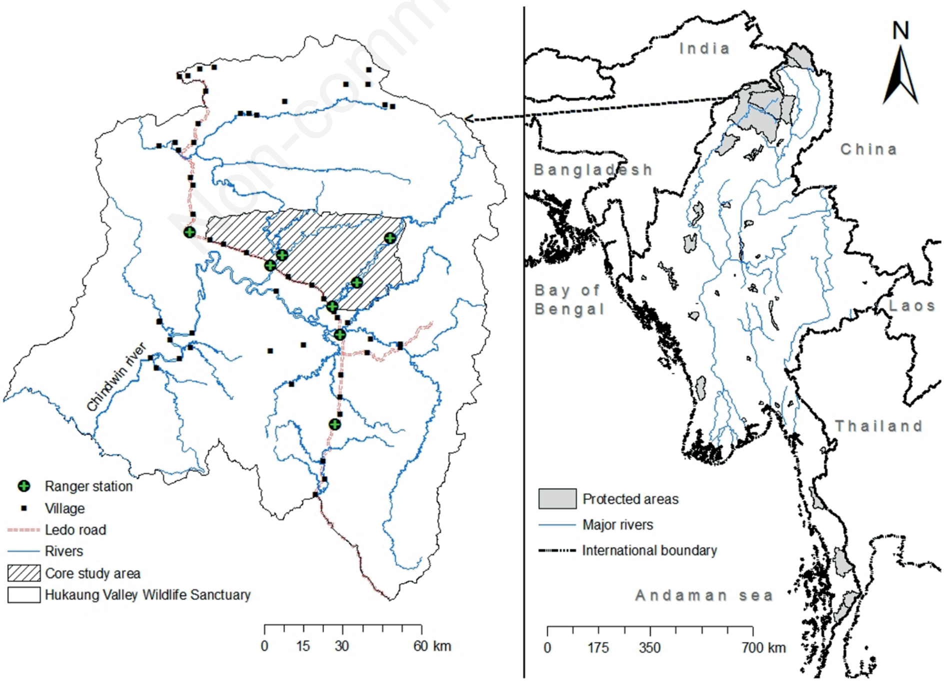

Figure 1. Location of Hukaung Valley Wildlife Sanctuary and Core study area (hatched) in Northern Myanmar.

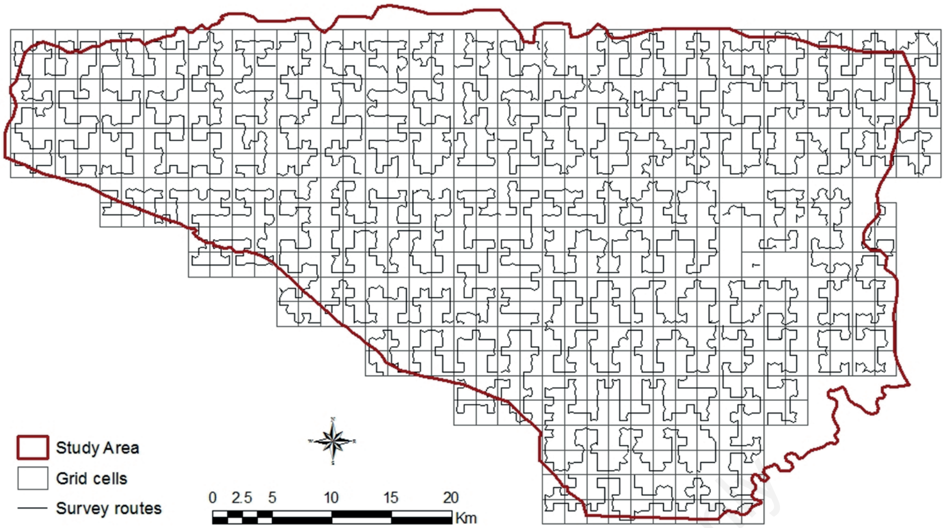

Figure 2. Survey routes of the occupancy survey conducted during December 2007 – May 2008 in the Core study area of the Hukaung Valley Wildlife Sanctuary of northern Myanmar.

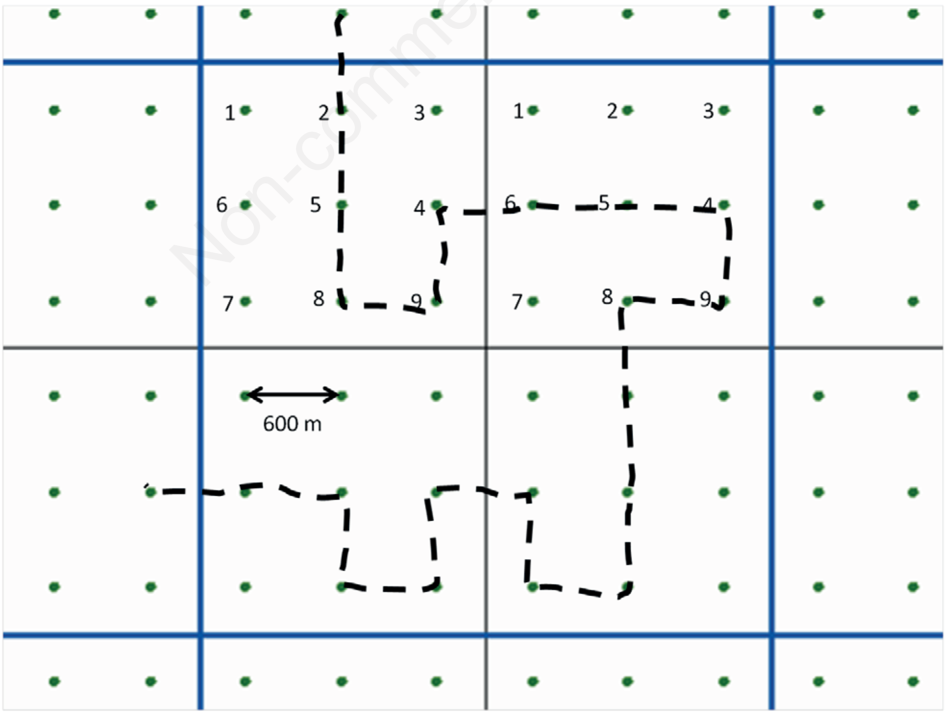

Figure 3. A sample survey route through 4 ~3.25 km² sub-grid cells (comprising 1 grid cell) searched for tiger prey species.

Data processing

During December 2007 and May 2008, presence-absence data (binary data) were collected using the occupancy survey method in the 1,800-km² of HVWS. Within the study area, 554 out of 564 grid cells (each with ten 300-m replicates) were searched, and tracks, pellets, and direct sightings were recorded. If the species of interest was present, it was counted as '1'; if it was not present (absence), it was counted as '0' in every spatial replicate.

For our modeling, we included environmental variables such as land cover types (Arino et al. 2012), elevation, slope, stream density, Euclidean distance to streams, mean monthly temperature, and mean monthly precipitation (Hijmans et al. 2005; Table 1), all calculated at the grid cell size. In addition, anthropogenic variables evaluated for prey occurrence and detection probabilities included Euclidean distance to roads, trails, ranger stations, and villages.

Predictor data were obtained from various sources, including the Myanmar Forest Department and Wildlife Conservation Society Myanmar Program, GlobCover 2009 ESA (300-m resolution; land cover classified as 22 types defined with the United Nations Land Cover Classification System), WorldClim (~21-km² resolution; mean monthly temperature and precipitation) and the Digital Elevation Model (SRTM90 data; 90-m resolution from USGS). Additional data from sign surveys were also used. Data collected on anthropogenic and environmental factors were compiled as spatially explicit indices using ArcGIS 10.1 (ESRI, CA, USA).

Land cover types were extracted from the GlobCover 2009 via ArcGIS online using spatial analyst extension ArcGIS 10.1 (Zonal statistics as a table) and classified as 12 types in the core study area (Table 2). We then calculated the exact proportion of each land cover type for each grid cell to assess the influence of each type on prey species occurrence. The mean elevation and slope for each site were extracted from the Digital Elevation Model (SRTM90 data with 90-m resolution from USGS) using spatial analyst extension of ArcGIS 10.1 (Zonal statistics as a table). Stream density was calculated using the field calculator in ArcMap in order to know the length of stream per square kilometer for each grid cell. Euclidean distance to the nearest stream was also calculated using spatial analysis extension of ArcGIS 10.1 (zonal statistics as a table). Euclidean distances to the road (located on the southern edge of the Core study area), trails (which were used by local tribes, wildlife and patrol rangers), and villages (located along the road) were calculated from the midpoints of site and spatial repli-

Table 1. Environmental and anthropogenic variables used in modeling prey distribution in the Core study area of the Hukaung Valley Wildlife Sanctuary of northern Myanmar.

Variable name	Description [range of values]
Cover types (habA-habL)	12 types (see Table 2)
Elevation (ele)	Mean altitude [203-554 m]
Slope (slp)	Mean slope [0°-33°]
Stream (stmD)	Stream density [0-3,600m/km²]
Stream (stm)	Euclidean distance to nearest stream [0-3,500 m]
Temperature (tem)	Mean monthly temperature [14.7-26.1°C]
Precipitation (pres)	Mean monthly precipitation [16-243 cm]
Trail (trl)	Euclidean distance to nearest trail [0-14,000 m]
Road (road)	Euclidean distance to nearest road [0-41,000 m]
Ranger station (rng)	Euclidean distance to nearest ranger station [0-21,000 m]
Village (vlg)	Euclidean distance to nearest village [0-42,000 m]

cates using spatial analysis extension of ArcGIS 10.1 (zonal statistics as table). The location of current ranger stations was plotted, and Euclidian distances were plotted to estimate variation in the potential effectiveness of protection (at each ranger station, there are 6 to 10 patrol rangers, of which 3 to 6 make regular patrols in their specified zone). Using spatial analysis extension of ArcGIS 10.1, we extracted the mean monthly temperature (°C) and precipitation (cm) from WorldClim (Hijmans et al. 2005) because of the high month-to-month variation (zonal statistics as a table).

Exploring data, building statistical models, and making inferences

Exploratory data analysis was done using program R (R 2.15.2, 2013). During data screening, all variables were then standardized (z-scores standardization) to improve interpretation. Predictor variables were tested for collinearity using the Pearson (r) correlation coefficient. Logistic regression was used to develop a single-season occupancy model (MacKenzie et al. 2002) for prey occupancy and detection data from sign survey. Each species (i.e, gaur, sambar deer, barking deer, and wild pig) was modeled using two logit functions: one for the probability distribution of occurrence (Ψ, 'psi'), and the other for the probability distribution of detection (p) contingent on occurrence. Program PRESENCE 6.2 (Hines 2006) was used for occupancy data analysis, and assumptions are as in MacKenzie et al. (2002).

Occupancy data analysis

For occupancy data analysis, we used the program PRESENCE (Version 6.2; Hines 2006). We applied a standard occupancy (single season) model (MacKenzie et al. 2002, Hines et al. 2010), which is based on two key parameters: 'site occupancy probability – Ψ (site level species occurrence probability)' and 'detection probability – p (spatial replicate level species detection probability of sites)'. We used Akaike Information Criteria (AIC) to compare and select models (Burnham and Anderson 2002). The maximum likelihood estimates of the model parameters were derived (MacKenzie et al. 2002, Hines 2006), and the top candidate models were used to predict habitat occupancy of gaur, sambar, muntjac, and wild pig. The results from the individual site occupancy estimates of the top candidate model was the real

Table 2. Abundance of land cover types in the Core study area of the Hukaung Valley Wildlife Sanctuary of northern Myanmar. Habitat ID is the letter code used in modeling.

Habitat ID	Land cover type	% cover
A	Rain-fed croplands	0.58
B	Mosaic croplands/vegetation	0.22
C	Mosaic vegetation/croplands	0.24
D	Closed-open broadleaved evergreen or semi-deciduous forest	78.91
E	Closed broadleaved deciduous forest	0.53
F	Open broadleaved deciduous forest	0.06
G	Closed needle-leaved evergreen forest	0.79
H	Closed-open mixed broadleaved and needle-leaved forest	1.14
I	Mosaic forest-shrub/ grassland	0.17
J	Closed to open shrub land	16.94
K	Closed to open grassland	>0.01
L	Water bodies	0.43

parameter estimate or the relative suitability of the site given the model predictions and was used to create a habitat occupancy map of each species using ArcGIS 10.1 software (ESRI, Redlands, CA, USA).

Results

In total, 1,651 km were walked and surveyed, and the detections of gaur, sambar, wild pig and muntjac were 878, 2,086, 350, and 1,953, respectively (total surveyed = 5,503 spatial replicates * 300 m). For guar and wild pig, we used the model with the lowest AIC despite there being other competing top models, as the only change was the inclusion or exclusion of a covariate for probability of detection, and our variables of interest, the PSI covariates, did not change. Thus, based on the top candidate model result, the potential covariates comprising the best candidate model for gaur were distance to the village, elevation, distance to the trail, habitat H (Closed-open mixed broadleaved and needle-leaved forest), habitat A (Rain-fed croplands), and distance to stream in site occupancy probability, and distance to the village in species detection probability (Table 3). The naïve occupancy estimate was 0.5162 (Figure 4), and the best candidate model result showed that 76% (SE=0.196) of the core study area could be occupied by gaur (Figure 5).

For sambar, factors included in the best candidate model were distance to the ranger station, distance to the small trail, distance to stream, stream density, distance to road, elevation, precipitation in site occupancy, and, for detection, distance to the small trail, distance to the ranger station, distance to stream, mean monthly precipitation, elevation, distance to road, and distance to the village (Table 3). The naïve occupancy estimate was 0.7762 (Figure 4) and, according to the best candidate model, sambar could occupy 91% (SE=0.03) of the core study area (Figure 5).

The covariates that most affected the distribution of wild pigs (Table 3) were distance to the ranger station, distance to the small trail, distance to stream at the site occupancy and distance to the ranger station, distance to road, distance to the village, and distance to trail. The naïve occupancy estimate was 0.3195 (Figure 4) and according to the best candidate model, the wild pig could occupy 57% (SE=0.003) of the core study area (Figure 5).

Table 3. Naïve occupancy estimate, site occupancy with standard error within brackets, positively and negatively correlated influencing factors on site occupancy and species detection of gaur, sambar, wild pig, and muntjac in the core study area of Hukaung Valley Wildlife Sanctuary of northern Myanmar by using standard occupancy (single season) model (MacKenzie et al. 2002, Hines et al. 2010).

Naïve	Occupancy		Covariate effects indicated	
Species	**Estimate**	**SE**	**Occupancy (Ψ)**	**Detection (p)**
Gaur	0.5162	0.76 (0.196)	Village (+), elevation (-), trail (-), HabH (-), HabA (+), stream (+)	Village (+)
Sambar	0.7762	0.91 (0.03)	Ranger (-), trail (-), stream (+), stream, density (+), road (+), elevation (-), precipitation (-)	Trail (-), ranger (-), stream (+), precipitation (-), elevation (-), road (-), village (+)
Wild pig	0.3195	0.57 (0.003)	Ranger (-), trail (-), stream (+)	Ranger (-), road (-), village (+), trail (-)
Muntjac	0.7996	0.89 (0.001)	Trail (-), village (+), ranger (-), HabD (+)	P (.)

The major influencing factors on muntjac distribution (Table 3) were distance to the small trail, distance to the village, distance to the ranger station, and habitat D (closed-open broadleaved evergreen or semi-deciduous forest) in site occupancy probability. The naïve occupancy estimate was 0.7996 (Figure 4), and the model result showed that muntjac could occupy 89% (SE=0.001) of the core study area (Figure 5).

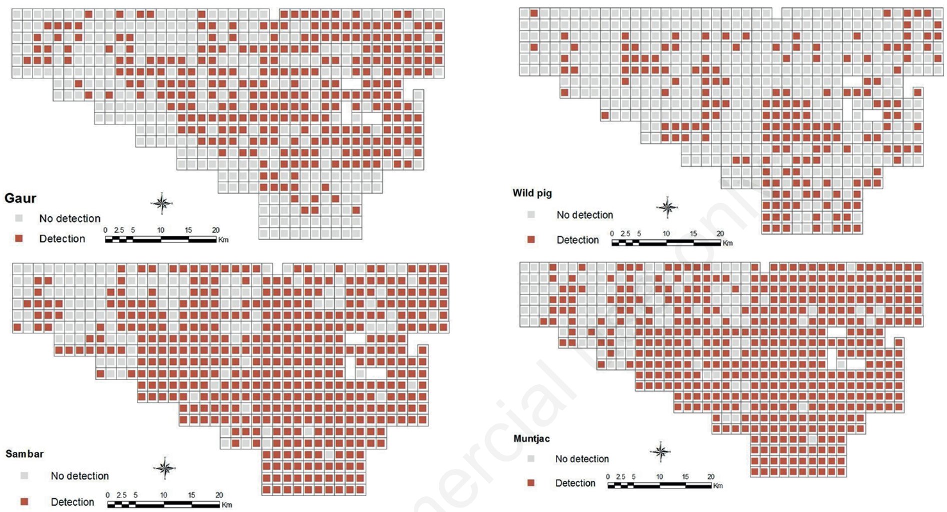

Figure 4. Naïve occupancy estimate of ungulates based on detection non-detection approach in the core study area of the Hukaung Valley Wildlife Sanctuary in Northern Myanmar.

Figure 5. Predicted site occupancy of tiger prey species using standard occupancy model in the core study area of the Hukaung Valley Wildlife Sanctuary in Northern Myanmar.

Discussion

Where poaching is not a limiting factor, prey biomass plays a critical role in tiger population viability (Karanth and Stith 1999). Based on reviews of tiger food habits (Hayward et al. 2012), as many as ten potential tiger prey species occur in the HVWS. In this study, three of the four tiger prey species most likely critical to tiger sustainability appeared to have relatively high occupancy rates. Still, wild pig occupancy seemed low given that the reproductive rate of wild pigs is the highest of any ungulate (Taylor et al. 1998), and they seem quite common wherever they occur.

Overall, tiger prey species occurrence was likely higher nearer ranger stations and trails and farther from villages (Table 4). These findings are are not surprising; areas nearest to ranger stations and trails commonly used by rangers patrolling for poachers likely have increased survival value (e.g., Jenks et al. 2012). Similarly, higher occupancy of some species in areas farther from villages and the main Ledo Road suggests that proximity to humans, in general, has negative influences because of easier access for hunters and poachers (e.g., Kilgo et al. 1998). Non-anthropogenic habitat factors were not identified as primary factors affecting distribution, though occupancy seemed to increase farther from streams; perhaps streams were used as travel ways by tigers avoiding humans, or even by poachers who avoid trails and thick vegetation. Since most of the core area was comprised of only 2 of the 12 cover types (closed to open mixed forest - 79%; closed to open shrub land - 17%), vegetation-related variables in the models should likely be viewed with caution. We note that it is also possible that open-mixed forest is critical to occupancy, but, given the lack of non-forested areas, it was not possibly to detect that signal.

In general, we found tiger prey occupancy increased farther from villages, at lower elevations, closer to trails and ranger stations, farther from streams and roads. Many of these findings parallel those in other studies. For example, Simcharoen et al. (2014) reported that in western Thailand sambar abundance was negatively associated with distance to the largest river in the study area, elevation, and the amount of dry deciduous dipterocarp forest cover and positively associated with relatively flat areas of river valleys. Jornburom et al. (2020) found that habitat use by both gaur and sambar was lowest in locations closest to human settlements, while gaur preferred steeper slopes at higher

Table 4. Summary of variable effects on modeling tiger prey distribution in the Core area of the Hukaung Valley Wildlife Sanctuary of northern Myanmar. Asterisk (*) indicates top ranked variable in the best model for the species.

Variable	Sambar	Wild pig	Muntjac	Gaur
Distance to ranger station	(-)*	(-)*	(-)	
Distance to trail	(-)	(-)	(-)*	(-)
Distance to village			(+)	(+)*
Distance to stream	(+)	(+)		(+)
Stream density	(+)			
Distance to road	(+)			
Elevation	(-)			(-)
Precipitation	(-)			
Closed-open mixed broadleaved			(+)	
Semi deciduous forest				(-)
Rain-fed cropland				(+)

elevations and sambar preferred lower slopes near streams. In an adjacent area of western Thailand, Phumanee et al. (2020) found gaur habitat use was most strongly influenced by proximity to saltlicks, sambar occupancy decreased from saltlicks and at higher elevations, wild pig occupancy was lower near villages, higher near saltlicks, and higher towards denser forest over more open habitats (from NDVI), and muntjac differed from the other ungulates in that none of the variables measured were statistically significant in predicting occurrence. In another adjacent area of western Thailand, Suksavate et al. (2022) reported that occupancy by gaur was most influenced by distance to the closest patrol path and road. Sambar was more likely occupying areas far from a reservoir, at a lower elevation, and in more open habitats, muntjac was less likely to occupy sites where humans were more common, and wild pigs occupied more areas away from roads and the reservoir. In the Western Ghats, India, gaur group density increased with larger available habitat and lower occurrence of livestock, sambar group density increased with higher mean slope and lower occurrence of livestock, and no variable could reliably explain wild pig group density (Punjabi and Rao 2017).

Tiger prey species appeared to occupy much of the study area and seem well distributed, especially in comparison (Table 5) with a very similar study in Lao PDR, where occupancy rates were also high (Vongkhamheng et al. 2013). However, similar to our study area, tiger abundance was very low there, making us wonder if high prey occupancy was equivalent to high prey abundance. In Nepal, Thapa and Kelly (2017) reported high prey occupancy and high tiger habitat use.

For comparative indices of prey abundance among areas with high and low tiger abundance, we examined data collected from camera-trap surveys in several areas with similar prey assemblages (Table 6). The results suggest that prey abundances and tiger abundance were positively related, except where tigers were known to have been eliminated through hunting. This also indicated that prey abundance in our study area was very low and likely unable to support many tigers. In fact, during the previous ten years, it appeared that both tigers and their prey had diminished substantially in our area (Naing et al. 2015), perhaps because of increased poaching after 2004 that seemed to correspond with large increases in the human population related to increased mining and agricultural developments.

Table 5. A comparison of modeled probability of site occupancy of tiger prey species from sign surveys and camera trap surveys in Southeast Asia.

	Sign surveys		Camera surveys		
	This study (2007-08)	Vongkhamheng et al. (2013)	Jornburom et al. (2020)	Phumanee et al. (2020)	Suksavate et al. (2022)
Species	**Myanmar**	**Lao**	**Thailand**	**Thailand**	**Thailand**
Muntjac	0.89	0.98	ns[a]	~0.68	0.77
Wild pig	0.57	0.93	ns[a]	0.59-0.80	0.29
Sambar	0.91	0.64	0.50	~0.25	0.31
Gaur	0.76	0.07	0.28	~0.20	0.29
Serow (*Capricornis milneedwardsii*)	ns[a]	0.43	ns[a]	ns[a]	ns[a]
Banteng (*Bos javanicus*)	ns[a]	ns[a]	0.56	ns[a]	0.10

[a]*Rare or not present in the area and thus not surveyed, or present but not surveyed.*

Conclusions

Management recommendations and future research

The management plan of Hukaung Valley Wildlife Sanctuary should be modified based on the habitat occupancy and detection probabilities of the principal tiger prey species we studied. The key positive influencing factors on species occurrence should be considered when strengthening future monitoring programs. In the Huakang Valley, sambar deer are eaten by local people in the area, and also sold to workers at the gold mines and in the concessions. Population reductions in sambar deer have been reported by groups that discussed their population trends (Papworth et al. 2017). Given this, ranger patrols should be increased (cf. Jenks et al. 2012), even if the number of ranger stations cannot be increased in the short term. The negative drivers of prey occupancy should be considered in planning strategic patrol station expansion, which should be increased at least double in the core study area.

For the long term, habitat management plans should be implemented, and based on the current baseline data related to biological and threat monitoring programs, future research should include a suitability analysis for new ranger stations, the interaction/conflict between livestock and wildlife (for example, wild pig and rain-fed cropland), the spatial quantity of domestic grazing, and human settlement and population growth in terms of both local people and itinerants in the Hukaung Valley. The role of the world-famous Ledo road should not be underestimated because it will probably be a critical East-West economic corridor for southern Asia, particularly between Myanmar's two giant neighbors, China and India.

To respond to probable impacts of climate change, a sustainable wildlife corridor and network system should be planned for. Fortunately, the Hukaung Valley Wildlife Sanctuary is well connected with three other wildlife sanctuaries and a national park under the Northern Forest Complex of Myanmar: Bum Hpabom Wildlife Sanctuary in the east, Hponkanrazi Wildlife Sanctuary, and Hkakaborazi National Park in the northeast. The last two are snow-capped mountain ranges linked to the Himalayan mountain ranges (Figure 1). In the lower part of Hukaung Valley is Htamanthi Wildlife Sanctuary, a tiger conservation protected area. Maintaining connectivity among these areas will assure a variety of habitats for wildlife into the future and, with adequate protection, may ensure viable tiger populations, as well.

Table 6. A comparison of photographic rate (photos per 100 trap nights) of tigers and prey species from camera trap surveys in Southeast Asia.

	Naing et al. (2015) Myanmar		Rao et al. (2005) Myanmar	Vinitpornsawan (2013) Thailand		Saisamorn et al. (2019) Thailand	Suksavate et al. (2022) Thailand		Rayam & Linkie (2015) Malaysia	
	HVWS	Core	HKBZ	TYNE	HKK	HKK	KSR	SLP	TFR	RBSP
Species	2001-04	2005-10	2002-03	2010-12	2010	2013 & 2015	2019-20		2009-11	
Tiger	0.5	<0.1	---[a]	1.5	3.4	4.4	---[d]	<1.0	0.9	2.4
Muntjac	6.8	3.8	18.1	22.7	13.2	18.8	3.6	8.1	6.7	25.0
Wild pig	1.3	0.8	10.7	3.5	7.3	2.1	3.8	8.8	4.2	6.8
Sambar	2.6	0.9	---[a]	10.0	9.8	15.8	0.3	4.8	<0.1	3.1
Gaur	0.3	0.8	---[b]	1.2	1.8	(2.2)[c]	0.4	1.1	0.15	0.25
Serow	<0.1	0.0	5.1	0.2	---[d]	---[d]	---[d]	---[d]	0.1	---[d]

[a]*Extirpated;* [b]*likely present but none recorded;* [c]*value for banteng;* [d]*rare or not present.*

Authors' contributions:

SHTP led field teams and ensured quality of surveys in the field while SH monitored quality of survey design and data. Under supervision of SH and SHTP, HN and the team carried out the field work and data entry. Preliminary data analysis was conducted by SHTP and SH with the support of WCS regional technical team, and HN conducted more advance data analysis. HN and TKF drafted the text, and all authors reviewed and commented on the submitted draft. All the authors have read and approved the final version of the manuscript and agreed to be held accountable for all aspects of the work.

Conflict of interest

The authors declare no potential conflict of interest.

Funding

None.

Availability of data and materials

Data is available upon reasonable request from the authors.

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References

Arino O, Ramos Perez JJ, Kalogirou V, Bontemps S, Defourny P, Van Bogaert E. 2012. Global Land Cover Map for 2009 (GlobCover 2009).© *European Space Agency (ESA) & Université catholique de Louvain (UCL)*, PANGAEA https://doi.org/10.1594/PANGAEA.787668

Barber-Meyer SM, Jnawali SR, Karki JB, Khanal P, Lohani S, Long B, MacKenzie DI, Pandav B, Pradhan NMB, Shrestha R, Subedi N. 2013. Influence of prey depletion and human disturbance on tiger occupancy in Nepal. *Journal of Zoology*. 289:10–18. https://doi.org/10.1111/j.1469-7998.2012. 00956.x

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L. 2001. Introduction to distance sampling. Oxford, United Kingdom: Oxford University Press. 448 pp.

Burnham KP, Anderson DR. 2002. Model selection and multi-model inference. 2nd ed. New York (NY), USA: Springer-Verlag. 514 pp.

Dinerstein E, Loucks C, Wikramanayake E, Ginsberg J, Sanderson E, Seidensticker J, Forrest J, Bryja G, Heydlauff A, Klenzendorf S, et al. 2006. The fate of wild tigers. *BioScience*. 57:508–514. https://doi.org/10.1641/B570608

Duangchantrasiri S, Jornburom P, Jinamoy S, Pattanavibool A, Hines JE, Arnold TW, Fieberg J, Smith JL. 2019. Impact of prey occupancy and other ecological and anthropogenic factors on tiger distribution in Thailand's western forest complex. *Ecology and Evolution*. 9:2449–2458. https://doi.org/ 10.1002/ece3.4845

Hayward MW, Jedrzejewski W, Jedrzejewska B. 2012. Prey preferences of the tiger *Panthera tigris*. *Journal of Zoology*. 286:221–231. https://doi.org/10.1111/j.1469-7998.2011.00871.x

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology.* 25:1965–1978. https://doi.org/ 10.1002 /joc.1276

Hines JE. 2006. PRESENCE- Software to estimate patch occupancy and related parameters. USGS-PWRC. http://www.mbrwrc.usgs.gov/software/presence.html

Hines JE, Nichols JD, Royle JA, MacKenzie DI, Gopalaswamy AM, Kumar NS, Karanth KU. 2010. Tigers on trails: occupancy modeling for cluster sampling. *Ecological Applications*. 20:1456–1466. https://doi.org/10.1890/09-0321.1

Jenks KE, Howard J, Leimgruber P. 2012. Do ranger stations deter poaching activity in national parks in Thailand? *Biotropica*. 44:826–833. https://doi.org/10.1111/j.1744-7429.2012.00869.x

Johnson A, Vongkhamheng C, Hedemark M, Saithongdam T. 2006. Effects of human-carnivore conflict on tiger (*Panthera tigris*) and prey populations in Lao PDR. *Animal Conservation.* 9:421–430. https://doi.org/10.1111/j.1469-1795.2006.00049.x

Jornburom P, Duangchantrasiri S, Jinamoy S, Pattanavibool A, Hines JE, Arnold TW, Fieberg J, Smith JL. 2020. Habitat use by tiger prey in Thailand's Western Forest Complex: What will it take to fill a half-full tiger landscape? *Journal for Nature Conservation*. 58:125896. https://doi.org/10.1016/j.jnc. 2020.125896

Karanth KU, Gopalaswamy AM, Kumar NS, Vaidyanathan S, Nichols JD, MacKenzie D. 2011. Monitoring carnivore populations at the landscape-scale: occupancy modelling of tigers from sign surveys. *Journal of Applied Ecology.* 48:1048–1056. https://doi.org/10.1111/j.1365-2664. 2011.02002.x

Karanth KU, Kumar NS, Srinivas V, Gopalaswamy A. 2008. Revised monitoring framework for Tigers Forever-Panthera sites. Technical Support Team-Tigers Forever. Bangalore, India: WCS-India.

Karanth KU, Nichols JD, Kumar NS, Link WA, Hines JE. 2004. Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences, USA*. 101:4854–4858. https://doi.org/10.1073/pnas.0306210101

Karanth KU, Stith BM. 1999. Prey depletion as a critical determinant of tiger population viability. In Siedensticker J, Christie S, Jackson P editors. Riding the tiger: tiger conservation in human dominated landscapes. Cambridge, United Kingdom: Cambridge University Press. p. 100–113.

Kilgo JC, Labisky RF, Fritzen DE. 1998. Influences of hunting on the behavior of white-tailed deer: implications for conservation of the Florida panther. *Conservation Biology.* 12:1359–1364. https:// doi.org/10.1111/j.1523-1739.1998.97223.x

Linkie M, Chapron G, Martyr DJ, Holden J, Leader-Williams N. 2006. Assessing the viability of tiger subpopulations in a fragmented landscape. *Journal of Applied Ecology*. 43:576–586. https://doi.org/ 10.1111/j.1365-2664. 2006.01153.x

Lynam AJ, Rabinowitz A, Myint T, Maung M, Latt KT, Po SHT. 2009. Estimating abundance with sparse data: tigers in northern Myanmar. *Population Ecology*. 51:115–121. https://doi.org/10.1007/s10144-008-0093-5

MacKenzie DI, Nichols JD, Lachman GB, et al. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology*. 83:2248–2255. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

Naing H, Fuller TK, Sievert PR, Randhir TO, Po SHT, Maung M, Lynam AJ, Htun A, Thaw WN, Myint T. 2015. Assessing large mammal and bird richness from camera-trap records in the Hukaung Valley of Northern Myanmar. *Raffles Bulletin of Zoology*. 63:376–388. http://zoobank.org/urn:lsid:zoobank. org:pub:89DE5E17293E42A69245579D86B291DB

Papworth S, Rao M, Oo MM, et al. 2017. The impact of gold mining and agricultural concessions on the tree cover and local communities in northern Myanmar. *Scientific Reports*. 7:1–11. https://doi.org/1 0.1038/srep46594

Phumanee W, Steinmetz R, Phoonjampa R, et al. 2020. Occupancy-based monitoring of ungulate prey species in Thailand indicates population stability, but limited recovery. *Ecosphere*. 11:e03208. https://doi.org/10.1002/ecs2.3208

Punjabi GA, Rao MK. 2017. Large herbivore populations outside protected areas in the human-dominated Western Ghats, India. *Mammalian Biology*. 87:27–35. https://doi.org/10.1016/j.mambio.2017.05.004

Rao M, Myint T, Zaw T, Htun S. 2005. Hunting patterns in tropical forests adjoining the Hkakaborazi National Park, north Myanmar. *Oryx*. 39:292–300. https://doi.org/10.1017/S0030605305000724

Rayan DM, Linkie M. 2015. Conserving tigers in Malaysia: A science-driven approach for eliciting conservation policy change. *Biological Conservation*. 184:18–26. https://doi.org/10.1016/j.biocon. 2014.12.024

Saisamorn A, Duengkae P, Pattanavibool A, Duangchantrasiri S, Simcharoen A, Smith JL. 2019. Spatial and temporal analysis of leopards (*Panthera pardus*), their prey and tigers (*Panthera tigris*) in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Folia Oecologica*. 46:73–82. https://doi.org/10.2478/ foecol-2019-0010

Simcharoen A, Savini T, Gale GA, Roche E, Chimchome V, Smith JL. 2014. Ecological factors that influence sambar (*Rusa unicolor*) distribution and abundance in western Thailand: implications for tiger conservation. *Raffles Bulletin of Zoology*. 62:100–106. http://zoobank.org/urn:lsid:zoobank.org:pub:3528409A-62CE-4F2D-8713-06D47FF98585

Steinmetz R, Chutipong W, Seuaturien N, Chirngsaard E, Khaengkhetkarn M. 2010. Population recovery patterns of Southeast Asian ungulates after poaching. *Biological Conservation*. 143:42–51. https:// doi.org/10.1016/j.biocon. 2009.08.023

Suksavate S, Dumsrisuk Y, Indarabut P, Godfrey A, Saosoong S, Harihar A, Samad I, Sukmasuang R, Duengkae P. 2022. Spatial and temporal habitat use by the main prey species of tigers in two protected areas of Thailand's Southern Western Forest Complex. *Environment and Natural Resources Journal*. 20:563–574. https://ph02.tci-thaijo.org/index.php/ennrj/article/view/247161

Taylor RB, Hellgren EC, Gabor TM, Ilse LM. 1998. Reproduction of feral pigs in southern Texas. *Journal of Mammalogy*. 79:1325–1331. https://doi.org/10.2307/1383024

Thapa K, Kelly MJ. 2017. Prey and tigers on the forgotten trail: high prey occupancy and tiger habitat use reveal the importance of the understudied Churia habitat of Nepal. *Biodiversity and Conservation*. 26:593–616. https://doi.org/10.1007/s10531-016-1260-1

Vié JC, Hilton-Taylor C, Stuart SN. (eds) 2009. Wildlife in a Changing World –An analysis of the 2008 IUCN Red List of Threatened Species™. IUCN, Gland, Switzerland. http://data.iucn.org/dbtw-wpd/edocs/RL-2009-001.pdf

Vinitpornsawan S. 2013. Population and spatial ecology of tigers and leopards relative to prey availability and human activity in Thung Yai Naresuan (East) Wildlife Sanctuary, Thailand. Ph.D. Thesis. USA: University of Massachusetts Amherst.

Vongkhamheng C, Johnson A, Sunquist ME. 2013. A baseline survey of ungulate abundance and distribution in northern Lao: implications for conservation. *Oryx*. 47:544–552. https://doi.org/10.1017/ S0030605312000233

Walston J, Robinson JG, Bennett EL, Breitenmoser U, da Fonseca GAB, Goodrich J, Gumal M, Hunter L, Johnson A, Karanth KU, et al. 2010. Bringing the tiger back from the brink - the six percent solution. *PLoS Biology*. 8:e1000485 https://doi.org/10.1371/journal.pbio.1000485

Online supplementary material:

Appendix 1. The best candidate models for gaur in the Core study area of the Hukaung Valley Wildlife Sanctuary of northern Myanmar.

Appendix 2. The best candidate models for sambar in the Core study area of the Hukaung Valley Wildlife Sanctuary of northern Myanmar.

Appendix 3. The best candidate models for wild pig in the Core study area of the Hukaung Valley Wildlife Sanctuary of northern Myanmar.

Appendix 4. The best candidate models for muntjac in the Core study area of the Hukaung Valley Wildlife Sanctuary of northern Myanmar.