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Ecological factors that influence sambar (*Rusa unicolor*) distribution and abundance in western Thailand: implications for tiger conservation

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Abstract. Prey density is declining throughout the tiger's (*Panthera tigris*) range and knowledge of the ecological factors that affect prey distribution and abundance remains surprisingly limited for this globally endangered species. In this study, we examined the ecological variables influencing the abundance of sambar (*Rusa unicolor*), the dominant prey species for the tiger across its global southern range. We also identified the scale at which these variables impact sambar distribution in Huai Kha Khaeng Wildlife Sanctuary, a high tiger density site in Southeast Asia. The fecal pellet group accumulation method was used to estimate an index of sambar abundance. Pellet groups were counted along 360 line transects randomly placed among four approximately 100 km^2 sites that encompassed six female tiger home ranges. The relationship between sambar pellet-group counts and 10 environmental variables was investigated using generalised linear mixed models. The sambar abundance index was negatively associated with distance to the largest river in the study area, elevation, and the amount of dry deciduous dipterocarp forest cover. Distribution and abundance of sambar were positively associated with relatively flat areas of river valleys, presumably due to the quality of vegetation available for foraging and greater visibility for detecting predators compared to other portions of the study area. This study is the first to identify the importance of wide alluvial valleys to tiger prey and suggests this habitat is critical for securing one of the largest tiger source populations in Southeast Asia.

Key words. *Panthera tigris corbetti*, tiger prey, habitat selection, Huai Kha Khaeng Wildlife Sanctuary

INTRODUCTION

Approximately 60% of the published studies on tiger (*Panthera tigris*) diet report that the sambar (*Rusa unicolor*) is the dominant prey species in terms of biomass in South and Southeast Asia (e.g., Seidensticker & McDougal, 1993; Karanth & Sunquist, 1995; Biswas & Sankar, 2002). Additionally, Hayward et al. (2012) reported that sambar are one of the two most preferred prey species throughout the entire range of tigers, and hypothesized that sambar importance in the tiger diet is a consequence of the nearly 1:1 predator to prey weight ratio between these two species, a common relationship reported for large cats. Ackerman (1986) provided an ecological rationale for this ratio in the mountain lion (*Puma concolor*) whereby a female needs to kill prey her size, or larger, to meet her own energetic requirements as well as those of her maturing offspring which can weigh as much or more than she does prior to their independence. Despite previous research on tiger diet and the proposed optimum prey size (Karanth & Sunquist, 1995; Hayward et al., 2012), studies (e.g., Ngampongsai, 1987; Padmalai et al., 2003; Matsubayashi et al., 2007 Bhattarai & Kindlmann, 2012) have rarely quantified the habitat preferences of the tiger's primary prey, the sambar. Understanding the habitat requirements of this species is clearly needed to predict the distribution and carrying capacity of tigers, and where appropriate, to manage the habitat to improve conditions for preferred prey. The sambar is also an important prey species because its widespread distribution in Asia largely overlaps that of the tiger in South Asia, South China and Southeast Asia (Corbett & Hill, 1992). Across its range, the sambar is highly adaptive; it occurs in a wide diversity of habitats, ranging from ocean shores to subalpine regions, and consumes a varied diet including coarse grasses, woody browse, broad-leaved foliage, fruit, and partially submerged water plants (Geist, 1998). In Thailand, sambar is the largest of the cervid species and historically it had the widest distribution in the region (Lekagul & McNeely, 1977; Francis, 2008). Given the significance of sambar in the diet of tigers and widespread documentation of prey depletion across the tiger's range, including Thailand (Ramakrishnan et al., 1999; Johnson et al., 2006; Datta et al., 2008), a better understanding of the ecological factors that influence sambar abundance and spatial distribution is needed in critical tiger habitats. The objectives of this study were to: 1) assess an index of abundance and distribution of sambar in the Huai Kha Khaeng Wildlife Sanctuary (HKK) a key site for tigers in western Thailand; and 2) identify ecological factors associated with sambar distribution. This information will provide conservation managers with a set

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of metrics to select and evaluate management actions for sambar and tigers.

MATERIAL AND METHODS

Study area. This study was conducted in HKK, which is located in western Thailand (15°00'–15°50'N, 99°00'–99°19'E) and represents the core of a forest complex consisting of 17 contiguous protected areas (collectively known as the Western Forest Complex or WEFCOM). This region supports the largest tiger population in Thailand (DNP, 2010). The sanctuary is 2,780 km^2 and elevation varies from 200–1,600 m. It has a tropical monsoonal climate with an annual temperature ranging from 8°C in January to 38°C in April. Total rainfall averages 1,386 mm (2000–2011), but most (78%) occurs in the wet season (May–October). From late November until April, dry season forest fires are common. This seasonal variation in temperature and rainfall results in a general dry deciduous forest mosaic. Depending on rainfall patterns, edaphic factors, and fire frequency, four primary vegetation types occur: mixed deciduous forest (48%); dry evergreen forest (25%); hill evergreen forest (13%); and dry deciduous dipterocarp forest (7%) (WEFCOM, 2004). A central feature of HKK is the 100 km long Huai Kha Khaeng River, which drains the central valley from north to south (Fig. 1). Many temporary and two smaller permanent streams originate in the rugged hills and empty into the main river. The lower part of this central valley is wide and less steep and is characterised by richer alluvial soils than the upper part of the valley. The HKK tiger population is currently estimated to be between 59–77 breeding individuals (DNP, 2010). Mean female home range size is 70 km^2 and mean male home range size is 267 km^2 (Simcharoen et al., 2014). The five major prey species of the tiger in HKK are banteng (*Bos javanicus*), sambar, gaur (*B. gaurus*), wild boar (*Sus scrofa*), and red muntjac (*Muntiacus muntjak*), but banteng, sambar, and gaur account for 87% of the biomass consumed by tigers (Petdee, 2000). In large parts of WEFCOM, however, sambar and other large prey species of tigers are absent or in decline (Steinmetz et al., 2010).

Sambar distribution and relative abundance. An index of sambar abundance was estimated by using the fecal pellet group accumulation method. This technique has been widely applied in ungulate habitat studies to obtain both absolute estimates as well as indices of deer abundance (Rogers et al., 1958; Mitchell et al., 1977; Bailey & Putman, 1981). The method is typically applied in habitats in which animals are difficult to count directly or where the assumptions of distance sampling are likely violated (e.g., in dense habitat animals secretively move from sight before being observed; Smart et al., 2004; Wegge & Storaas, 2009). Because > 70% of the habitat in HKK (e.g., dry evergreen forest, mixed deciduous forest) has dense ground cover, we assumed that sambar would be difficult to count directly. Field work was conducted during the dry season (November–April) between 2009 and 2011.

Within the Wildlife Sanctuary we focused our investigation on deer distribution and relative abundance in areas located within four sites where home ranges of tiger have been studied (Fig. 1). This deer survey was primarily designed to investigate food availability in different tiger home ranges to represent the array of ecological diversity within the sanctuary. These sites cover about 14% of the total sanctuary area and represent the three major forest types present (we excluded hill evergreen forest which covers approximately 13% of the sanctuary). Although not optimal, we are confident that data obtained in this survey can be cautiously used to explain the sambar distribution in the entire sanctuary. Each of the four sites is approximately 100 km^2 encompassing six female tiger home ranges. These sites were also chosen to represent the range of ecological conditions in HKK that might reflect differences in both deer density and tiger home range size. Two sites (KBD and KYD) were in the central valley of the sanctuary along the lower and upper portions of the Huai Kha Khaeng River. The other sites (KNR and KPP) were drier areas away from Huai Kha Khaeng River. For this project, deer sampling did not include the full range of the ecosystems found in the WEFCOM, but was limited to a subsample due to the intensive sampling needed to estimate sambar numbers and the limited budget and personnel. Specifically, we did not sample the roughly 22% of HKK above 900 m because sambar are rarely observed in this steep terrain (Trisurat et al., 2010). At each site we

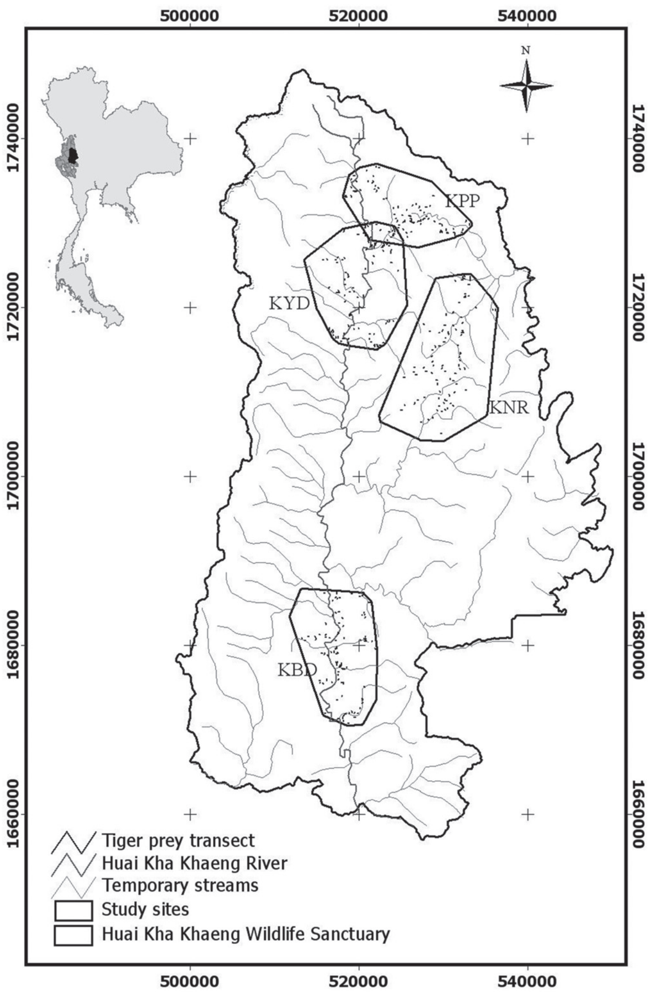

Fig.1 Location of Huai Khaeng Wildlife Sanctuary in western Thailand and the 360 sampling units contained within the four areas represent six female tiger home ranges.

randomly located 90 transects each forming a 200 × 200 m square, totalling 800 m in diameter, for a total of 360 square transects across the four sites. In each square transect, we place 40 circular plots, each measuring 20 m^2, approximately 20 m apart (for a total of 3,600 plots per site and 14,400 plots in total). We cleared plots of all pellet groups and then returned to the plots after 30 days to estimate the rate of pellet group accumulation. Pellet groups were counted and distinguished from each other following Simcharoen et al. (2014). We considered the total number of pellet groups divided by the total number of transects as an index of sambar abundance and number of sambar pellet groups within each transect as an index of habitat use.

Ecological variables. Based on previous work by Trisurat et al. (2010) and our knowledge of the species, we identified 10 ecological variables which we hypothesized to potentially influence sambar distribution and abundance in HKK. Nine were derived using a GIS database prepared by the Western Forest Complex Ecosystem Management Project, Department of National Parks, Wildlife and Plant Conservation (WEFCOM, 2004). Variables included terrain ruggedness, slope, elevation (m), distance to all streams (m), distance to Huai Kha Khaeng River (m), distance to a salt lick (m), and average low slope patch size (areas with slopes shallower than 10%). Because Rotenberry et al. (2006) emphasised the need to consider multiple scales in habitat use studies we measured slope and the average low slope patch size at two scales (150 and 600 m radius from the center of each transect). These scales are our best estimate of the range of areas in which ecological variables would attract a sambar to the vicinity of our transects. Vegetation type was recorded during our field surveys and classified for each of the 1,440 circular plots. For each circular plot we recorded vegetation type as either mixed deciduous forest (MD), dry deciduous dipterocarp forest (DD), dry evergreen forest (DE) or bamboo forest (BB). The habitat type for each square transect was assigned as the proportion of the habitat types recorded in its 40 circular plots. Bamboo was later lumped with mixed deciduous forests both in our square transects and in the overall forest type availability map in the WEFCOM GIS. Terrain ruggedness was measured as a vector ruggedness measure (VRM) using an ArcView script. Ruggedness values range from 0 (no terrain variation) to 1 (complete terrain variation). The value of natural terrain ranges from 0–0.4 (Sappington et al., 2007). We defined “slope” as the median slope and the “average low slope patch size” as the total low slope area within a 150 m and 600 m radius.

Data analysis. We investigated the relationship between sambar pellet-group counts (response variable) and the above 10 environmental variables using generalised linear mixed models with negative binomial error terms. We did not standardise these variables when performing the regression analyses. To reduce possible effects of multicollinearity, we discarded one independent variable of each tested pair if the between variable association had an r-value>0.5 (Torres et al., 2011).The choice of which correlated variable to remove was based on the relative strength of its Pearson correlation with the frequency of pellet counts. The remaining independent variables were then added to the model. We also investigated the interaction between the distance from Huai Kha Khaeng River and the elevation as a variable because our previous experience suggested that both tigers and sambar avoided higher elevations near the main river. We accepted the model with the lowest AIC value as the best representation of the relationship between pellet group counts and ecological factors (Burnham & Anderson, 2010). The analysis was performed using the MASS package (Venables & Ripley, 2002) in program R (R Core Team, 2012).

RESULTS

Sambar distribution and index of abundance. We searched sambar pellet groups on a total of 360 square transects in four sites representing six female tiger home ranges that ranged from 200–900 msl in altitude and included three main habitat types recorded in HKK: 75.3% MD, 8.9% DD, and 15.7% DE. Habitat proportions for each site were 72% MD, 5% DD, and 23% DE for KPP; 73% MD, 9% DD, and 18% DE for KYD; 70% MD, 21% DD, and 9% DE for KNR; and 88% MD, 2% DD, and 10% DE for KBD. The median slope for the square transects ranged from 0–23%. Sambar pellet groups were found in 63% of all square transects. In total, we recorded 1,041 pellets groups (102 in KPP, 444 in KYD, 26 in KNR, and 469 in KBD). Per habitat type we recorded 48 pellet groups in DD forest, 246 in DE forest, and 747 in MD forest. The mean number (±SD) of pellet groups recorded in all square transects was 2.9±4.6. The mean number of pellets in a pellet-group was 32±14. The relative abundance of sambar in HKK was 3,615±3,180 pellet groups km^{-2}. A Mann-Whitney U test was used to examine the effect of distance to the main river on sambar pellet abundance. There was a significant difference in the median number of sambar pellet groups in the square transects of KBD and KYD, sites located close to the Huai Kha Khaeng River (Fig. 1; median=3 pellet groups square $transect^{-1}$; abundance=6,340±245 pellets group km^{-2}), and the median in the other two sites KNR and KPP, located further from the Huai Kha Khaeng River (Fig. 1), (median=0 pellets group square $transect^{-1}$; abundance=889±746 pellets group km^{-2}); (Mann-Whitney U test, Z=−9.31, p=0.05, n=180).

Ecological variables. Results from the correlation tests suggested that sambar pellet abundance had a strong negative association with the distance to the Huai Kha Khaeng River (r=−0.34, p<0.0001). Sambar pellets were negatively associated with the occurrence of dry deciduous dipterocarp forest (r=−0.16, p=0.001) and positively associated with the average low slope patch size within a 600 m radius (r=0.16, p=0.001) and 150 m radius of square transect centers (r=0.14, p=0.004). Terrain ruggedness was discarded from the variables tested because it was highly correlated with slope (r=0.76) and slope was more correlated with pellet group abundance. The remaining nine ecological factors were deemed to be uniquely associated with pellet group counts (Table 1). Following model selection, only three of the ecological variables (dist. hkk, DD, and elev) were included in the best-fit model (Table 2). Our top model suggests that the interaction between distance to the main river and elevation

Table 1. Variables used to identify factors potentially affecting sambar (*Rusa unicolor*) distribution and their levels of significance (Pearson correlations).

Variable	p-value	r-value
Distance to main stream (dist.hkk)	<0.001	−0.340
Average low slope patch size of 600 radius (patch.600)	0.001	0.166
Habitat type : dry dipterocarp (DD)	0.001	−0.162
Average low slope patch size of150 radius (patch.150)	0.004	0.140
Elevation (elev).	0.080	−0.092
Habitat type : Mixed deciduous (MD)	0.100	0.086
Distance to salt lick (salt lick)	0.500	−0.035
Slope 600 radius (slp.600)	0.729	−0.018
Slope 150 radius (slp.150)	0.733	−0.017
Habitat type : Dry evergreen (DE)	0.770	0.015
Distance to any stream (dist.st)	0.995	0.0003

Table 2. Candidate models of sambar (*Rusa unicolor*) occurrence in Huai Kha Khaeng Wildlife Sanctuary, Thailand. Here we report Akaike's Information Criterion values (AIC), the difference in AIC rank relative to the top model (ΔAIC), the relative model weights (w_i), the number of parameters in the model (k), and the model deviance (Dev.). Full variable names and abbreviations are listed in Table 1.

Candidate Model	AIC	ΔAIC	w_i	k	Dev.
Dist.hkk*elev+DD	1446.2	0	0.56	6	359.2
Dist.hkk+DD	1447.9	1.7	0.24	4	360.1
Dist.hkk+DD+patch.600	1448.7	2.5	0.16	5	360.4
Dist.hkk+patch.600	1452.5	6.3	0.02	4	361.3

Table 3. Regression coefficient estimates and standard errors (SE) for the top-supported models for sambar abundance (Table 2, model 1).

Variable	Estimate	SE
intercept	2.417e+00	3.307e-01
dist.hkk	−5.860e-04	1.296e-04
elev	−1.714e-03	6.793e-04
DD	−2.445e-02	1.040e-02
dist.hkk*elev	6.222e-07	2.838e-07

affect sambar abundance (regression parameter estimate for the interaction of dist.hkk*elev.=6.22×10^{-7}, SE=2.84×10^{-7}, p<0.01). Sambar abundance was greatest at low elevations near the Huai Kha Khaeng River (Fig. 2; Table 3). Sambar abundance was negatively associated with increases in DD habitat (regression parameter estimate for DD=-2.44 x10^{-2}, SE=2.84×10^{-2}, p<0.01)

DISCUSSION

This study examined sambar distribution and index of abundance at landscape and micro scales in relation to habitat variables and it focused on habitats typical of the core area of the tiger population in Thailand's Western Forest Complex. Our results indicated that the distribution and index of abundance of sambar in HKK was related to distance from the main river (Huai Kha Khaeng River) and elevation; abundance was greater in areas closest to the main river at lower elevations where the predominant habitat type is mixed deciduous forest. In addition, dry deciduous dipterocarp was negatively correlated with the index of abundance. This could be related to a lower defecation rate in this habitat type however, we do not have evidence to support this interpretation.

Sambar abundance. Sambar is an important tiger prey species and is preferred in the diet of tigers throughout Southeast and South Asia (Hayward et al., 2012). Historically, sambar occurred throughout the tiger's range, with the exception of northern China and the Far East of Russia where it is replaced by a close relative, the red deer, *Cervus elaphus*, (Miquelle et al., 2010, Hayward et al., 2012). However, sambar is one of several large mammal species that has recently experienced major declines primarily due to habitat degradation and poaching (Wikramanayake et al., 1998, Linkie et al., 2003, O'Brien et al., 2003) and is now consider globally threatened (Timmins et al., 2008). Pellet groups were used as an index of sambar abundance. Although it is important not to assume that indices are automatically linked to the actual abundance of the species, we felt that fecal accumulation provides a reasonable estimate of relative abundance because it appeared that decomposition rates were similar across habitat types.

Ecological variables. We examined nine ecological variables hypothesized to predict sambar pellet abundance. Pellet group abundance appeared to be correlated with distance to Huai Kha Khaeng River. The river valley is topographically flatter than the rest of the sanctuary and it has a relatively high percentage of grass species (Kruuk et al., 1994). Shrestha (2004) reported that ungulates in lowland Nepal prefer similar low-lying areas, particularly flood plains with grass and riverine forests. Trisurat et al. (2010) noted that sambar avoid steep terrain and prefer open habitat; Bagchi et al.

(2003) also suggested that sambar preferred grassland and dense shrubs closer to water in India. Additionally, McKay & Eisenberg (1974) noted that sambar are sedentary and do not shift their ranges seasonally. Our study aimed to model sambar distribution in relation to ecological variables and to identify the importance of wide alluvial valleys to tiger prey.

Distance to the main river had the highest correlation with pellet group abundance, but it is important to note that, in contrast, there was no correlation of deer pellet abundance to distance of smaller permanent streams. It is clearly not water itself that makes the main river attractive to sambar; instead, a complex of ecological parameters derived from other geologic and geographic features of the valley likely produce a desirable mixed deciduous forest habitat. Gallery forests, the typical habitat along the Huai Kha Khaeng river, described as both seasonally flooded areas and non-flooded areas of mixed deciduous forest (Chimchome et al., 1998), might have a higher food availability due to the constant water supply (Budke et al., 2008) compared to the same habitat type found away from this permanent water source. Moreover, this habitat had denser understudy vegetation

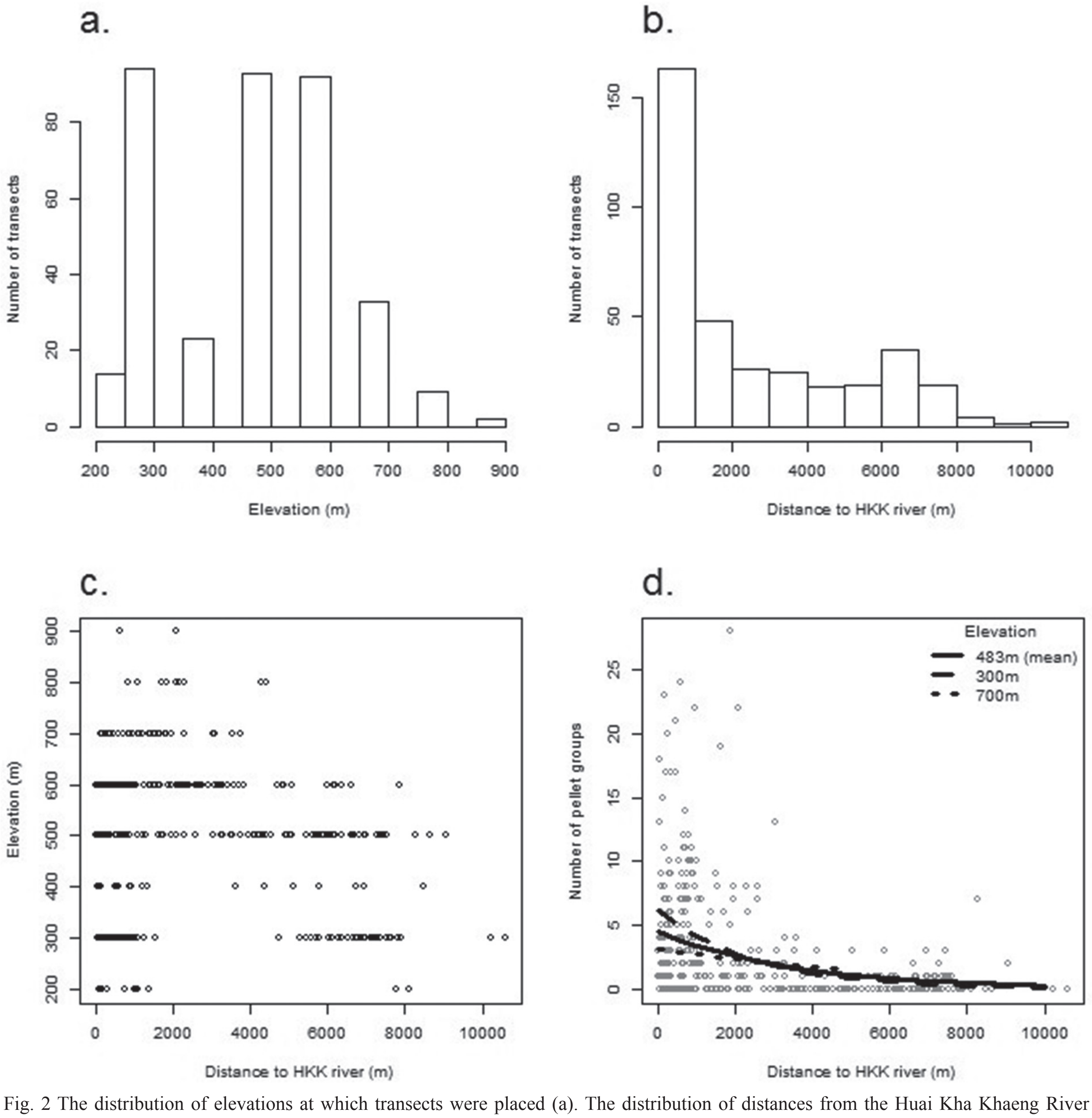

Fig. 2 The distribution of elevations at which transects were placed (a). The distribution of distances from the Huai Kha Khaeng River (HKK) at which transects were placed (b). The combinations of elevation and distance to HKK River at which pellet groups were found (each dot represents a single transect) (c). The number of pellet groups found in relation to distance from the HKK River at three elevations (where dots represents transects) (d). Dots represent transects and lines represent the predicted number of pellet groups using our top-supported model (Table 2, model 1) solved at mean covariate values and one of three elevations to illustrate the interaction of elevation with distance to the HKK River**.**

which might offer better concealment from predators. On a geological time scale, gradual erosion has likely deposited richer soils near the main river resulting in the growth of more nutritional ungulate forage in this zone. Similarly, higher soil moisture is more likely at lower elevations near the main river. These two factors are represented in the interaction between the main river and elevation. Soil quality and moisture might also be expected to affect food availability following Shrestha's (2004) observation of sambar preference for the flood plains of Nepal and similarly in India sambar's preference for lower elevations (Bagchi et al., 2003).

Although overall presence of water was not highly correlated with sambar numbers, lack of water combined with poorer soils found in dry deciduous dipterocarp forest may account for the lower density of sambar in this vegetation type. The negative response to dry deciduous dipterocarp may reflect a seasonal shift of sambar away from this habitat. For example, Srikosamatara (1993) reported that sambar density in HKK in the dry season was lower than the wet season. However, even in the wet season ground cover is limited and grass is much sparser in dry deciduous dipterocarp forest (Smitinand, 1977). The lower relative abundance of sambar in dry deciduous dipterocarp forest versus mixed deciduous forest is further indicated by a preliminary analysis of long-term camera trapping data where detection in DD was two times lower than in MD (S. Duangchantrasiri, unpublished data). Finally, a study in Nagarahole India demonstrated that the density of sambar in mixed deciduous forest habitat was seven times that of dry deciduous dipterocarp forest (Karanth & Sunquist, 1992). Therefore, a number of factors appear to make this forest type less attractive to sambar than the alluvial valleys.

Conservation implications. Our results have subtle but important implications for sambar and tiger conservation. With widespread prey depletion occurring globally in response to habitat degradation and poaching (Sanderson et al., 2002; Linkie et al., 2003; O'Brien et al., 2003), increased patrolling and other forms of management (e.g., restoration of degraded land, management on trans-boundary lines between tiger ranges) to reduce human impacts are needed. Given financial constraints, it is important to target sambar management efforts in areas where there is likely to be a reasonable return for conservation efforts. For example, investment to restore sambar numbers in rugged terrain in Kuiburi National Park, Thailand, met with little success (Steinmetz et al., 2009). Our study suggests that even with significant effort, such rugged habitat is not likely to support a dense population of sambar. We recommend that prime areas to target should be the wide interior valleys of the WEFCOM, and elsewhere in Asia where the habitat is more favorable. In WEFCOM, some of these valleys, though they occur in wildlife sanctuaries, are currently used by small villages that inhabited the area before it was designated as a wildlife sanctuary. Our results suggest that these valleys should be a high priority for management because the habitat is suitable and lie within the area of the largest source population of tigers in Southeast Asia (Walston et al., 2010).

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