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Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape

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Abstract

We examine the abundance and distribution of Sumatran tigers (*Panthera tigris sumatrae*) and nine prey species in Bukit Barisan Selatan National Park on Sumatra, Indonesia. Our study is the first to demonstrate that the relative abundance of tigers and their prey, as measured by camera traps, is directly related to independently derived estimates of densities for these species. The tiger population in the park is estimated at 40–43 individuals. Results indicate that illegal hunting of prey and tigers, measured as a function of human density within 10 km of the park, is primarily responsible for observed patterns of abundance, and that habitat loss is an increasingly serious problem. Abundance of tigers, two mouse deer (*Tragulus* spp.), pigs (*Sus scrofa*) and Sambar deer (*Cervus unicolor*) was more than four times higher in areas with low human population density, while densities of red muntjac (*Muntiacus muntjac*) and pigtail macaques (*Macaca nemestrina*) were twice as high. Malay tapir (*Tapirus indicus*) and argus pheasant (*Argusianus argus*), species infrequently hunted, had higher indices of relative abundance in areas with high human density. Edge effects associated with park boundaries were not a significant factor in abundance of tigers or prey once human density was considered. Tigers in Bukit Barisan Selatan National Park, and probably other protected areas throughout Sumatra, are in imminent danger of extinction unless trends in hunting and deforestation are reversed.

INTRODUCTION

Tigers (*Panthera tigris*) are behaviourally flexible and may adapt to a host of alterations in their landscape (Sunquist, Karanth & Sunquist, 1999). Tigers range from sea level to altitudes of 2000 m, and habitats include the savannas of India, equatorial rainforest of Southeast Asia and the pine forests of eastern Russia. Sunquist (1981) and Karanth & Nichols (2000) showed that tigers in Nepal and India can tolerate close proximity to human settlements. Their high fecundity allows for rapid recovery from poaching (Karanth & Stith, 1999) as long as there is sufficient prey. A broad diet, including ungulates, bovids and primates, allows tigers to live wherever large mammalian prey species are available (Seidensticker, 1986; Karanth & Sunquist, 1995; Miquelle *et al*., 1999; Ramakrishnan, Coss & Pelkey, 1999). Not surprisingly, prey depletion is a critical threat to the long-term persistence of tigers (Seidensticker, 1986; Karanth & Stith, 1999).

Despite their ecological flexibility, tigers are critically endangered throughout their range (Seidensticker, Christie & Jackson, 1999), and three subspecies have been driven to extinction. Two of these subspecies, the Bali (*P. t. balica*) and the Javan (*P. t. sondaica*) tiger, have been eliminated from their respective Indonesian islands primarily through habitat loss. Prey population reduction and direct killing of tigers, however, may have been the final *coup de grâce* for these subspecies (Seidensticker, 1986, 1987). The Sumatran tiger (*P. t. sumatrae*), the only remaining Indonesian tiger, persists in isolated populations across Sumatra. Sumatran tigers experience many of the threats faced by tigers throughout their range, including direct poaching, loss of prey, forest conversion and human–tiger conflicts leading to authorized removals of 'problem tigers' (Tilson *et al*., 1994; Dinerstein *et al*., 1997; Seidensticker *et al*., 1999). The degree to which these threats affect Sumatran tigers may vary (Tilson *et al*., 1994), but little work has been done to assess the relative importance of these threats to their long-term persistence.

Dinerstein *et al*. (1997) proposed a plan for identifying high-priority areas for tiger conservation (called Tiger Conservation Units, or TCUs) and argued that conservation efforts should target these areas. One criterion for a high-priority TCU is large size with an adequate core area (in general, > 2000 km^2). Karanth & Stith (1999) however, point out that tigers may not persist in TCUs as large as 3000 km^2 if the prey base is inadequate. Unfortunately, we have little information on

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the status of tigers in many of these TCUs, and even less information on the prey base. This lack of knowledge hampers tiger conservation effectiveness not only in Indonesia but also throughout Asia.

In 1994, Indonesia developed a tiger conservation strategy (Ministry of Forestry, 1994) that mandated conservation action based on a comprehensive understanding of tiger ecology, but to date few studies have addressed the status of wild tiger populations on Sumatra (Franklin *et al.*, 1999). In the past decade, land clearing has accelerated dramatically (Holmes, 2001; Kinnaird *et al.*, 2003), and tiger poaching has increased (Plowden & Bowles, 1997; H. T. Wibisono, unpubl. data), but the direct impact on tigers remains unquantified. In this study, we assess the distribution and abundance of tigers and their prey in the Bukit Barisan Selatan National Park (BBSNP), a little-known but high-priority TCU in southern Sumatra, Indonesia. Specifically, we test camera trap-based abundance indices proposed by Carbone *et al.* (2001: but see Jennelle, Runge & Mackenzie, 2002 and Carbone *et al.*, 2002) against independently derived density estimates, and use these indices to examine the distribution and abundance of tigers relative to prey availability, park boundaries and density of human population.

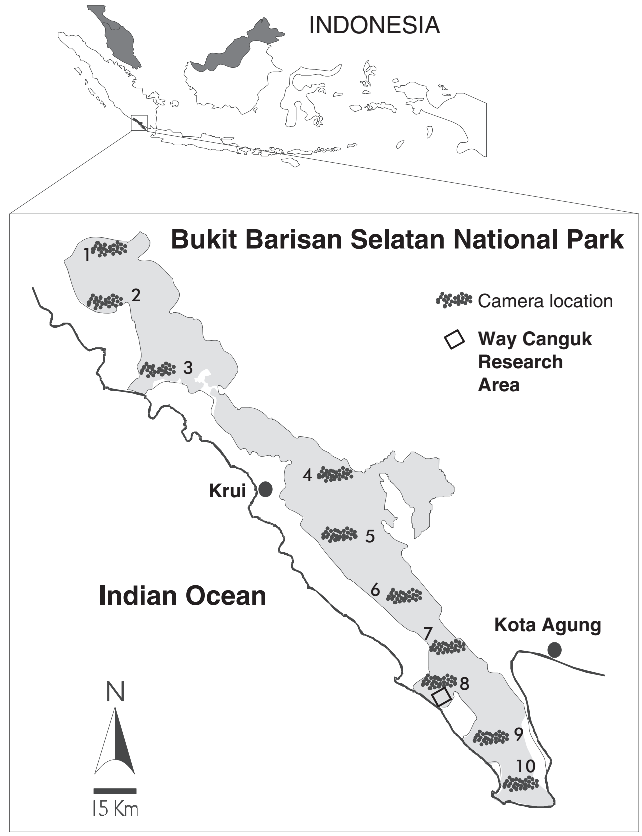

Fig. 1. Location of Bukit Barisan Selatan National Park in Sumatra, Indonesia. Camera trap survey was conducted in the numbered sampling blocks. All line transect data and camera trap abundance index calibration were collected in Way Canguk research area. Tiger density estimate was based on data collected in Way Canguk and sampling blocks 7 to 10.

METHODS

Study area

Bukit Barisan Selatan National Park (BBSNP) is the third-largest protected area (3568 km^2) on the Indonesian island of Sumatra (Fig. 1). Located in the extreme southwest of the island (4° 31′ to 5° 57′ S and 103° 34′ to 104° 43′ E), the park covers more than 150 km of the Barisan Mountain Range. BBSNP contains some of the largest tracts of lowland rainforest remaining on Sumatra and is the major watershed for southwest Sumatra. The park is bordered by villages, agriculture and plantation forestry. The park's thin shape results in > 700 km of borders where encroachment for logging and agriculture and illegal hunting are major problems. Rainfall is seasonal, ranging from 3000 mm to more than 4000 mm except during ENSO events when droughts occur. Temperatures fluctuate from 22 to 35°C.

The Way Canguk Research Station is located in the southern part of BBSNP (5° 39′ 32″ S, 104° 24′ 21″ E; Fig. 1) at 50 m elevation, in a mosaic of primary forest, and forest damaged by fire, drought, wind throws and earthquakes. The associated study area encompasses 900 ha of forest, is bisected by the Canguk River and is crossed by trails at 200 m intervals. The area is contiguous to large tracts of undisturbed lowland forest as well as areas disturbed by illegal logging and agricultural activity.

Camera trapping

We conducted tiger and prey surveys using passive infrared camera traps (CamTrak South Inc., Watkinsville, GA 30677) with data packs that stamp each photograph with time and date of the event. Cameras were set in 10 × 2 km sampling blocks orientated from forest/park boundary towards park interior in order to detect potential edge effects on mammals. Sampling blocks were spaced uniformly at 10–15 km intervals south to north except in a narrow isthmus of heavily degraded forest in the north-central part of the park (Fig. 1). In the northernmost block, rugged terrain and *Albhizzia* plantation encroachment limited use of the rectangular design and traps were set in a 4 × 5 km block. Each block was divided into 20 subunits of 1 km^2, and a random UTM coordinate was chosen within each subunit. We randomized our sample design to reduce bias in the abundance indices and chose a 1 km^2 'mesh' for our sample to assure that no tiger home range could fit between cameras (see Karanth & Nichols, 1998). Single cameras were placed at 'optimal' locations within 100 m of the UTM coordinate and new coordinates were taken using a Brunto XLS 1000 GPS unit. 'Optimal' locations were usually animal trails with signs of recent activity. An additional three to four pairs of camera traps were deployed opportunistically within the sampling block at points where tigers were likely to pass, especially on trails below a ridgeline, trails near water and passages between hills. Each camera pair was positioned to photograph simultaneously both flanks of an animal passing by the sensors. These nonrandom camera placements were used to increase the possibility of photographing tigers and of identifying left-flank and right-flank photographs taken with single-set cameras. Cameras were mounted on trees such that the infrared beam was set at a height of 45 cm. Each unit was programmed to delay sequential photographs by 45 seconds and operate 24 hours/day or until the film was fully exposed.

Owing to the roadless nature of most of the park, access was difficult and we were unable to check the function of cameras during a sampling period to monitor performance or change films. Cameras were left in the forest for 30–35 days. Number of trap-days was calculated for each camera location from the time the camera was mounted until the camera was retrieved if the film had remaining exposures, or until the time and date stamped on the final exposure. After cameras were retrieved, films were developed and examined for tigers and prey. We identified each photo of an animal to species, recorded the time and date, and rated each photo as a dependent or independent event. We defined an independent event as (1) consecutive photographs of different individuals of the same or different species, (2) consecutive photographs of individuals of the same species taken more than 0.5 hours apart, (3) nonconsecutive photos of individuals of the same species. We used number of independent photographs of a species as an index of species abundance and calculated two relative-abundance indices (RAI). The number of days required to acquire a photograph (RAI_1) measured effort and was expected to decrease as density increased (Carbone *et al.*, 2001). The inverse of RAI_1 was the number of photographs acquired per day (RAI_2) and increased as density increased, making it an easily interpreted index. RAI_2 was scaled to photographs per 100 trap-days.

The Way Canguk research area was sampled on three occasions between September 1998 and October 1999 to compare camera trap abundance indices with line transect density estimates for the same location. At 6-month intervals, we deployed camera traps at a density of 1 trap/16 ha throughout the study area. Cameras were left in place for approximately 30 days and then retrieved.

Capture–recapture estimate of tiger abundance

We followed methods developed by Karanth (1995) and Karanth & Nichols (1998) to estimate tiger abundance and density from camera photos using CAPTURE Program (Otis *et al*, 1978; White *et al.*, 1982; Rexstad & Burnham, 1991) and data collected in the southern part of the park at five sites between September 1998 and February 1999. We used data only from the southern part of the park because these data were collected during a restricted time period (6 months) and the southern section is a peninsula with limited possibilities for immigration and emigration. Because CAPTURE produces population estimates based on closed-population assumptions, use of data from the southern section of the park gave greater confidence in geographic and demographic closure.

We established capture histories for each tiger identified in the photographs. Because most camera locations used only one camera, however, we restricted our analysis to animals photographed only on the left side. Although this approach usually results in lower probabilities of capture (P) compared to using two cameras/location, it is still possible to use this method for estimation (Karanth, 1995; J. D. Nichols, pers. comm.). Capture history for a tiger consisted of a row of zeroes (no photograph) and ones (photographs) indicating the result of each sampling interval of trapping for a tiger. A sampling interval was the result of a single day of trapping at each of the camera locations (up to a maximum of 34 trapping occasions at each of five sampling blocks). Following Karanth & Nichols (1998), we used CAPTURE Model M_h that allows variability in capture probability among individuals but assumes constant capture probability for a given individual over time.

Line transects

We estimated prey densities for one avian and six mammal species using line transect sampling (Table 1: Burnham, Anderson & Laake, 1980; Buckland *et al.*, 1993; Laake *et al.,* 1993). Each month, from June 1998 to December 1999, three pairs of observers walked 18 transects in the Way Canguk Research Area over a 3-day period for a total of 38 km. Transects were walked each day by observer pairs spaced at 400 m intervals, beginning at 0600 and ending at approximately 0930. We recorded total length of transect walked and, for each species, number of clusters detected. For each cluster, we noted the number of animals, sighting distance and sighting angle. We calculated quarterly density estimates by combining census data for a 3-month period that centred on the month of camera trapping in the study area. Prey densities and standard errors were estimated from line transect data using Fourier Series Estimator (Burnham *et al.*, 1980; Buckland *et al.*, 1993) which is generally regarded as a robust density estimator (Krebs, 1989).

Calibrating camera data

For relative abundance indices to be useful, there should be a monotonic relationship between the index and actual density (Conroy, 1996). To test this relationship, we compared the number of days required to obtain single independent photographs (RAI_1; Carbone *et al.*, 2001) of tiger and six diurnal or crepuscular prey during three camera trapping periods in Way Canguk with line transect density estimates of prey species in Way Canguk and the capture–recapture estimate of tiger density (tigers were not observed during line transect surveys) for the southern peninsula of the park where Way Canguk is located.

We analyzed the relationship between the RAI_1 and density estimates using linear regression and reduced major axis regression (Sokal & Rohlf, 1981; Harvey & Pagel, 1991). Reduced major axis regression minimizes the sum of the products of horizontal and vertical deviations from points on the line, allowing for error in the independent variable. This has the advantage of accurately estimating the true functional relationship, but produces residuals that are usually correlated with the independent variable. Linear regression models always have shallower slopes than reduced major axis regression models because they assume no error in the independent variable, but the difference between the two regressions is small when the coefficient of determination is high (Harvey & Pagel, 1991).

Human and edge effects

We calculated the distance from each camera location to the nearest park boundary and grouped camera locations into 1 km intervals. To assess the relative abundance of tigers and prey in areas of differing human density, we assumed that human density was correlated with village density. Village populations around BBSNP range from 500 to 7500 with an average of 2530 people/village (SE = 290, N = 29 villages; WCS-IP, unpubl. data). We counted number of villages within 10 km of park boundaries in 10 km increments from south to north. We then classified each camera location as adjacent to an area of high or low human density based on number of villages within 10 km of park boundaries at the approximate latitude where cameras were placed. Areas of low human density were defined as having <10 villages (average human population < 25,000) and areas of high human density were defined as > 15 villages (average human population > 37,500). We then compared mean photos/100 trap-days (RAI_2) in samples adjacent to high and low human densities at varying distances from the park boundary using ANOVA and ANCOVA (Sokal & Rohlf, 1981).

RESULTS

Camera trap performance

We deployed 370 cameras during the survey and calibration trials. Of these, 84.3% had unexposed film remaining at the end of the sampling period. Of the remaining cameras, 5.1% finished the film within the final week of the sampling period, 3.2% finished the film within 8–14 days of pickup, and 1.9% finished the film within 15–21 days of pickup. Only 5.4% of the cameras finished the film or misfired in the first week of the sampling period, were lost, or were damaged by elephants rendering them useless. This translates into an average failure rate of 1.5 cameras/sample. Given the density of camera placement, we believe that the low failure rate was unlikely to influence trapping coverage or bias indices derived from the camera trap data.

Table 1. Sampling effort for estimating tiger abundance in the southern part of Bukit Barisan Selatan National Park in 1998–99 for five locations

Site	Date	Duration (in days)	# tigers (recaptures)	Camera points	Trap-days
Way Canguk	9/98	21	1(1)	38	700
Pemerihan	10/98	34	1(0)	24	742
Blambangan	11/98	32	1(0)	24	711
Paya	1/99	34	4(2)	22	737
Sukaraja	2/99	31	2(0)	21	650

Density estimates and calibration of camera data

We identified nine individual tigers from 12 photographs of left flanks, based on a total of 2873 trap-days at five sample locations (Table 1). Using CAPTURE model M_h, we estimated a capture probability (P-hat) of 0.0271 for the tiger data set. The estimated population size for the sample is 13 ± 3.66, with a 95% confidence interval of 10–27 individuals. To determine density we assumed the effective sampling area to be equal to the area defined by the sides of the sampling blocks, plus a buffer strip equal to the longest distance between recapture photographs (4.5 km for this data set). The estimated sample area was calculated at 836 km^2 and the average density for the southern portion of BBSNP was estimated at 1.6 tigers/100 km^2 (95% CI = 1.2–3.2 tigers/100 km^2; Table 2).

Table 2. Activity patterns, density estimates (/km^2) and percent coefficient of variation for tigers and selected prey species by sampling method. Date indicates the month in which the sampling was initiated.

Name	Method	Date	Density	% CV	Activity
Tiger *Panthera tigris*	Capture/recap.	Nov 98	0.0156	27.56	Diurnal
Argus pheasant *Argusianus argus*	Line transect	Sept 98	1.76	37.5	Diurnal
		Apr 99	0.91	21.9	
		Sept 99	3.33	60.0	
Mouse deer *Tragulus* spp.	Line transect	Sept 98	6.28	36.8	Crepuscular
		Apr 99	2.74	34.7	
		Sept 99	2.00	194.0	
Red muntjac *Muntjac muntiacus*	Line transect	Sept 98	3.96	31.5	Crepuscular
		Apr 99	4.44	25.6	
		Sept 99	1.76	27.8	
Sambar deer *Cervus unicolor*	Line transect	Sept 98	0.88	51.1	No pattern
		Apr 99	1.42	47.9	
		Sept 99	0.62	79.0	
Pigtail macaque *Macaca nemistrina*	Line transect	Sept 98	5.04	31.9	Diurnal
		Apr 99	2.6	49.6	
		Sept 99	5.65	33.1	
Wild pig *Sus scrofa*	Line transect	Sept 98	6.06	43.3	Diurnal
		Apr 99	4.4	45.4	
		Sept 99	4.6	77.4	

Prey densities based on line transect estimates varied widely among species and over time (Table 2). Densities range from 0.49 individuals/km^2 for sambar deer to 6.28 individuals/km^2 for combined mousedeer species. On average, pigtail macaques are the most common prey species, followed by mousedeer and red muntjac. Coefficients of variation ranged from 22% to 194%, indicating a broad spectrum of precision associated with density estimates. Much of the variability may be due to changes in encounter rates over time associated with different species, and small sample sizes associated with some estimates (n < 20 for seven of 18 estimates). In addition, macaque and wild pig group ranges extended beyond the study area boundaries (9 km^2) and consequently groups could be missing from the study area during some surveys. Finally, the density estimates also may underestimate group-living species if undercounts of groups occurred.

Way Canguk cameras were active for a total of 2904 trap-days during 21, 30 and 30-day sample periods. We used the natural logarithm of density estimates from line transects and CAPTURE to develop a regression analysis of number of trap-days required to photograph an individual of a single prey species (RAI_1) on transformed density. The linear regression indicated a close negative relationship between the RAI_1 and density ($RAI_1 = 106.8 - 59.8 \times \text{Ln(density)}$, $F_{1,14} = 45.71$, $P < 0.0001$, $r^2 = 0.79$ (Fig. 2). Reduced major axis regression produced a steeper slope for the relationship; $RAI_1 = 111.4 - 68.32 \times \text{Ln(density)}$, but slopes and intercepts of the two regression lines are not significantly different, indicating that number of photos provides a reliable density index for tigers and their prey in BBSNP.

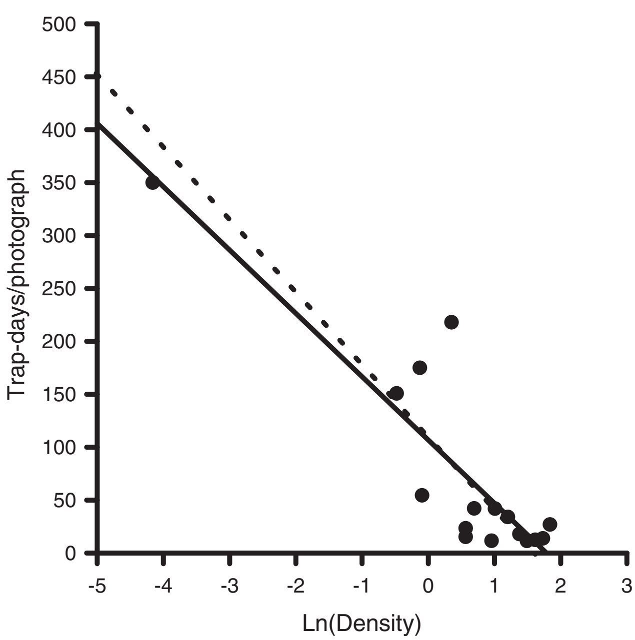

Fig. 2. Linear regression (solid line) and reduced major axis regression (dashed line) of number of days required to take one photograph as a function of the natural logarithm of estimated density. Data are for tigers and six prey species reported in Table 2.

The value of 350 trap-days to photograph a single tiger appeared to be an outlier. We tested the value using a one-sided Grubbs' statistic (Sokal & Rohlf, 1981) for testing outliers and found that the tiger data point was not a significant outlier. Second, we compared regressions with and without the tiger datum. Although the coefficient of determination (r^2) declined when the tiger datum is removed, the slope and intercept did not change significantly (RAI_1,w/out tiger = 110.5 – 63.7Ln(density)). We therefore retained the point because it reflects the range of densities and trapping effort in the study.

Park-wide camera surveys

We conducted ten surveys over 20 months for 6973 camera-trap-days. We exposed 2074 frames and classified 1665 frames as independent photographs. Among the photographs, we captured seven bird species, 34 mammal species from a minimum of 19 families (most rodent families excluded) and one reptile.

We photographed 1684 individuals of nine prey species (Table 3). Although additional prey species such as jungle fowl, rodents, moonrats and treeshrews were identified, we did not include them in this analysis because they were small (< 1 kg) and were rarely (< 5 photos) photographed. RAI_2 values (expressed as photos/100 trap-days) for prey ranged from 0–1.90 photos/100 trap-days for the uncommon sambar deer, to 1.85–22.51 photos/100 trap-days for the group-living pigtail macaques. Tigers were photographed on 20 occasions (19 single animals, one pair) at 17 locations in eight of ten surveys. The RAI_2 for tigers varied from 0 to 0.95 photos/100 trap-days. Tigers, argus pheasant and the deer species were each absent from at least one sampling block. Mean RAI_2 values are less than the median for all species, indicating abundance distributions are skewed towards 0.

The RAI_2 of many of the prey species co-vary. Mouse deer RAI_2s are significantly correlated with all other diurnal/crepuscular prey species except argus pheasant

Table 3. Number of independent photos and mean and range of relative abundance index values (RAI_2) for tiger and prey in BBSNP.

Common name	# photos	Mean	Range
Tiger *Panthera tigris sumatrae*	20	0.29	0–0.95
Great argus pheasant *Argusianus argus*	193	2.78	0–7.08
Pigtail macaque *Macaca nemistrina*	618	7.95	1.85–22.51
Common porcupine *Hystrix brachyura*	200	2.72	0–6.88
Malay tapir *Tapirus indicus*	92	1.25	0.14–4.99
European wild boar *Sus scrofa*	265	3.53	0.13–9.84
Greater and lesser mouse deer *Tragulus* spp.	87	1.16	0–3.66
Red muntjac *Muntiacus muntjac*	185	2.45	0–6.33
Sambar deer *Cervus unicolor*	40	0.55	0–1.90

(Table 4). Red muntjac indices are positively correlated with sambar deer and pigtail macaque indices, and wild pig indices are significantly correlated with sambar deer and pigtail macaque indices. Tiger abundance varies with the abundance of large prey. Tiger RAI_2 is correlated with RAI_2 of pigs (Table 4: $P < 0.05$) and Sambar ($P < 0.1$), the largest primary-prey species. A regression of the RAI_2 of tigers on the sum of the RAI_2 of pigs and sambar is significant and positive ($RAI_{2,\mathrm{Tiger}} = 0.109 + 0.043(RAI_{2,\mathrm{pig+sambar}})$, $T = 3.72$, $P = 0.045$).

Human density and edge effects

Number of villages adjacent to the park was higher (16 to 30 villages) for samples 3, 4, 5, 6 and 7 (Fig. 1), compared to other sampling areas (0–9 villages). We therefore classified these blocks as high human-density areas. Tiger RAI_2 was four times higher in areas of low human-density compared to high density (Fig. 2). Similarly, the RAI_2 of large prey species were 5.6 (sambar) and 9.5 (pig) times higher in low human-density samples. Among smaller prey, mouse deer and pigtail macaque were 9.7 and 2 times more common, respectively, in low human-density samples. Only argus pheasants and Malay tapir were more common in samples adjacent to high human density.

We used two-way ANCOVA to assess the importance of edge effects and human density on the relative abundance of tigers while controlling for the relative abundance of large prey, and two-way ANOVA to assess edge and human effects on relative abundance of prey. Data were summarized for each species as RAI_2 in 1 km intervals from the park boundary in for each sample with high and low human density adjacent to the park. When controlling for the effect of human density and distance from the edge, the abundance of large prey did not significantly affect RAI_2 of tigers and was dropped from the model. In general, human density adjacent to the sampling area had a larger effect on RAI_2 of tigers and prey compared to distance from park boundaries. Tiger RAI_2 was significantly higher in low human-density areas ($F_{1,36} = 4.609$, $P = 0.039$), as was pig abundance ($F_{1,36} = 14.495$, $P < 0.001$), sambar deer ($F_{1,36} = 4.765$, $P = 0.036$), and mouse deer ($F_{1,36} = 9.128$, $P = 0.005$). Human density had no significant effect on RAI_2 of red muntjac, pigtail macaques, porcupines and Malay tapir. Edge effects were significant only for red muntjac ($F_{7,36} = 2.71$, $P = 0.023$) and mouse deer ($F_{7,36} = 3.312$, $P = 0.008$); these species were more abundant at 0–1 km from the park boundary. The significance of the interaction term for mouse deer ($F_{7,36} = 3.382$, $P = 0.007$) and the trend for red muntjac ($F_{7,36} = 2.124$, $P = 0.06$) indicate the boundary effect is due to high abundance close to the boundary in areas with low human density.

DISCUSSION

Photographs from camera traps have been used by Karanth (1995) and Karanth & Nichols (1998, 2000) in combination with mark–recapture models to determine tiger densities in India. More recently, Carbone *et al.* (2001) used photographic capture rates from studies of tigers across their range in conjunction with computer simulations to show that camera trap abundance indices may provide good estimates of tiger density. Carbone *et al.*'s study, however, was limited by the lack of independent density estimates using standard capture–recapture or line transect methods for comparison and was criticized by Jennelle *et al.* (2002; but see Carbone *et al.*, 2002). Our study is the first to demonstrate that the relative abundance of tigers and their prey, as measured by camera traps, is directly related to independently derived estimates of densities for these species. We believe that the results of the relative abundance analysis reflect real differences in the abundance and distribution of tigers and their prey in BBSNP.

We estimated tiger density for the BBSNP peninsula at 1.6 tigers/100 km^2. If we apply the regression to photographic accumulation rate for tigers across the entire park (RAI_1 = 349 trap-days/photo), we predict the park density at 1.7 tigers/100 km^2. The density estimates expand to a park population estimate of 54–59 tigers older than 1 year of age. This estimate, however, is based on the unlikely assumption that the entire park is suitable tiger habitat. Conversion of forest to agriculture within park boundaries has increased dramatically in the past decade; Kinnaird *et al.* (2003) calculate that 28% of the forest cover has been lost between 1985 and 2000. A more conservative estimate, therefore, may be 40–43 tigers, assuming that tigers require forest cover in BBSNP and

Table 4. Pearson Correlation matrix (N = 10) among relative abundance values (RAI_2) of tigers and prey

	Tiger	Mouse deer	Muntjac	Sambar	Pigtail	Pig	Argus	Porcupine	Tapir
Tiger	XX								
Mouse deer		XX							
Muntjac		0.772**	XX						
Sambar	0.578*	0.793***	0.754**	XX					
Pigtail		0.818***	0.632**		XX				
Pig	0.620**	0.900***		0.653**	0.692**	XX			
Argus							XX		
Porcupine								XX	
Tapir									XX

* $0.05 < P < 0.1$
** $P \le 0.05$
*** $P < 0.01$

that the deforested agricultural areas represent marginal or unsuitable habitat.

Tilson *et al.* (1994), using population viability analysis, predicted that a population of 68 tigers in BBSNP would have a high probability of persistence over the next 100 years. This result was based on a poaching rate of one tiger/year, no habitat loss, no prey depletion and no natural catastrophes. Doubling of the poaching rate to two tigers/year would drive the BBSNP tiger population to extinction within the next 100 years, and possibly within the next 50 years. Lindzey *et al.* (1992, 1994), however, state that large cats may survive hunting mortality of up to 25% annually, and modelling by Karanth & Stith (1999) suggest that these figures are relevant to tigers. If we follow Karanth & Stith's model, the present BBSNP tiger population could withstand the elimination of five to six tigers/year in the absence of habitat loss and prey depletion.

Available data indicate that poachers in the BBSNP have killed at least 32 tigers since 1998 (Kompas, 1999; H. T. Wibisono, unpubl. data), averaging more than eight tigers/year. Clearly, the high estimated level of tiger poaching is unsustainable under any condition. We believe, however, that depletion of prey and habitat are additional factors accelerating the disappearance of tigers from BBSNP.

Although we were unable to measure hunting of prey directly in this study, indirect measures of hunting including snares, cartridges, discarded batteries, gunshots, direct observation of hunters and sale of bushmeat and wildlife parts (Peres, 2000; Wright *et al.*, 2000) were all observed in BBSNP or adjacent villages and cities. Additionally, a national sport-hunting club, *PERBAKIN*, openly operates in and around BBSNP and their activities include the commercial sale of bushmeat, primarily wild pig (Tempo, 2000). A number of studies have linked human density to declining wildlife populations, often owing to hunting (Peres, 2000; Woodroffe, 2000; Harcourt, Parks & Woodroffe, 2001; Parks & Harcourt, 2002). If we assume that the human density on the perimeter of the park directly reflects per capita hunting then our results are consistent with the expectation that hunting by humans has a strong influence on the distribution and abundance of prey species in the park. Under this assumption, we would expect the observed pattern of lowest abundance of wildlife in sample areas 4–7 (Fig. 1) where human density is highest. The ratios of species abundance in areas of low and high human densities are severely skewed (Fig. 3); hunted species are significantly more abundant in the sample areas with low human density adjacent to the park.

The influence of human density extends to habitat loss. Kinnaird *et al.* (2003) show that forest conversion has been most severe between sample areas 3 and 7 (Fig. 1), areas of high human density. They conclude that the amount of secure habitat in BBSNP available for large mammals such as tigers is shrinking faster than measures of forest loss indicate, because wildlife is more vulnerable at the forest edge. Tigers and many prey species that normally use edges may be subjected to increased vulnerability to hunting on the park boundaries where human density is high. Additionally, the park has become fragmented and BBSNP tigers may now comprise two small, isolated subpopulations. If true, the tigers of BBSNP are more vulnerable to stochastic demographic events (Lande, 1988).

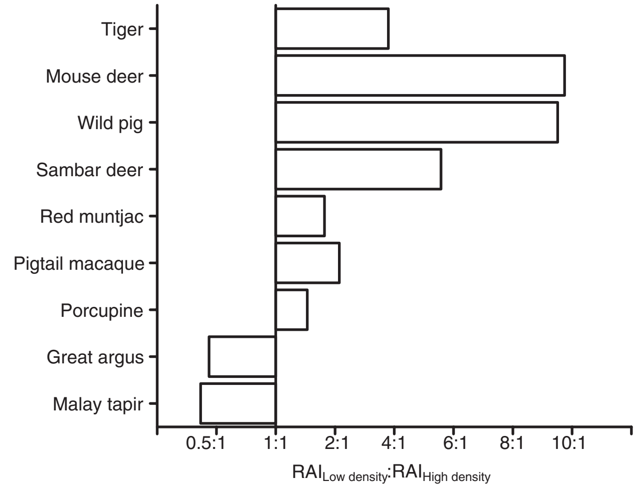

Fig. 3. Ratio of average relative abundance indices (RAI_2) for tigers and prey in low human-density samples compared to high human-density samples.

Although forest loss may ultimately eliminate BBSNP tigers, there is still enough forest in the park today to protect viable populations of deer with ranges of a few square kilometers and tigers with ranges of as much as 100–200 km^2. Hunting pressure, however, will eliminate tigers and prey populations much more rapidly than habitat loss alone. In the short term, park management should focus on curbing illegal hunting of tigers and their prey. Solutions should include better enforcement, control of bushmeat trade and sport-hunting activity, and better control of domestic trade in tiger parts. Indonesia, unfortunately, is experiencing a prolonged financial and political crisis and decentralization of natural-resource management that makes increasing the commitment to conservation in general (Jepson *et al.*, 2001), and to tiger conservation in BBSNP in particular, very difficult. International conservation groups (Wildlife Conservation Society, World Wildlife Fund, National Fish and Wildlife Foundation), private donors and the US Fish and Wildlife Service are supporting tiger conservation action in BBSNP. These actions include monitoring of tiger and prey populations and habitat, support of anti-poaching patrols, increasing awareness of local communities, and working with local governments to modify land-use plans and consider conservation as a planning objective. The Indonesian government, especially at the provincial and district level, needs to show willingness to sustain these conservation activities if the BBSNP tiger population is to survive into the future. On a larger scale, failure to act now in BBSNP and other Sumatran protected areas may result in Indonesia having the dubious distinction of driving a third subspecies of tiger to extinction.

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