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Conservation status of tigers in a primary rainforest of Peninsular Malaysia

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Abstract

This study provided the first reliable density estimate of tigers based on photographic capture data in Taman Negara National Park, Peninsular Malaysia's most important conservation area. Estimated densities ($\overline{X} \pm$ SE) of adult tigers ranged from 1.10 ± 0.52 to 1.98 ± 0.54 tigers/100 km^2 ($X^2 = 1.56$, df = 2, $P = 0.46$) with the overall mean of 1.66 ± 0.21 tigers/100 km^2. The tiger population in the 4343-km^2 park was estimated to be 68 (95% CI: 52–84) adult tigers. Prey biomass estimates ranged from 266 to 426 kg/km^2, and wild boar were the most important potential prey species in terms of abundance, biomass, and occupancy, followed by muntjac. Both tigers and leopards were more diurnal than nocturnal, which corresponded with the activity patterns of wild boar and muntjac. No evidence of poaching of large mammals was found in the 600-km^2 study sites and overall human impacts on the tiger–prey community appear to be minimal, but in the long run its viability needs to be evaluated in a greater landscape context.

Keywords: Tigers; Population estimation; Mark-recapture models; Camera trapping; Malaysia

1. Introduction

The tiger *Panthera tigris* is a highly adaptable species and exhibits tolerance to a wide range of forest types, climatic regimes, altered landscapes and prey bases (Schaller, 1967; Sunquist et al., 1999; but see Kerley et al., 2003). Today, many of the remaining tiger populations are confined to small and isolated forests (Dinerstein et al., 1997) where stochastic events and continuing human impacts are likely to cause local extinction (Smith et al., 1987). Even tiger populations in large forest tracts may not be secure (Kenney et al., 1995), especially those in tropical rainforest habitats where prey densities are naturally low (Eisenberg and Seidensticker, 1976).

The ecology and conservation status of tigers are least known from the Indochinese region (i.e., Vietnam, Cambodia, Thailand, Laos, Myanmar, and Malaysia). This paucity reflects the difficulty of studying elusive, forest-dwelling animals in regions marked by political instability and social upheavals over the past several decades (Rabinowitz, 1999). Efforts are underway in several range states to improve our knowledge of the status of Indochinese tigers, and this research represents the first scientific study of the ecology of tigers in Malaysia.

Malaysia occupies the southern limit of the distribution of mainland tiger populations. In the past century, Malaysia lost half of its forest cover and most of the remaining forests are located primarily in mountainous regions with little agricultural value or in isolated protected areas. Since independence in 1957, large areas of productive lowland forests have been converted to oil palm and rubber plantations through government agricultural development schemes. In addition to habitat loss and fragmentation, increased demands for wild meat and high-priced body parts of some wild animals have reduced populations of many large mammals. The Javan rhinoceros *Rhinoceros sondaicus* and banteng *Bos javanicus* are already extinct and the Sumatran rhinoceros *Dicerorhinus sumatrensis* is critically endangered (Aiken and Leigh, 1992).

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The recent declines in tiger numbers across its range are also evident in Malaysia, where tiger numbers declined from an estimated 3000 in the early 1950s (Locke, 1954) to 250 in the early 1980s (Khan et al., 1983). Since 1976 tigers have been totally protected under the Protection of Wildlife Act. Possibly due to the better protection, the estimated population doubled within a decade from 250 to 500 tigers (Khan, 1987; Topani, 1990). Asserting that the estimate was conservative, the figure was adjusted to 600–650 (Khan, 1987). Although these figures have been cited widely (Nowell and Jackson, 1996; Seidensticker et al., 1999; Sunquist and Sunquist, 2002), the traditional census technique, which relies on counting subsamples of tracks to estimate animal abundance, lacks scientific rigor; and thus it is not reliable in evaluating threats and conservation efforts (Karanth et al., 2003).

The existing protected area system in Peninsular Malaysia relies heavily on its only national park, Taman Negara National Park. It was established between 1938 and 1939, and, largely due to its inaccessibility the park has remained relatively intact and undisturbed. It encompasses 4343 km^2, accounting for 59% of the total protected area in Peninsular Malaysia and is not only the largest park among 13 national parks in the nation (12 other parks are in East Malaysia) but also one of the largest in Southeast Asia.

Taman Negara is part of a large contiguous tract of forest that stretches to southern Thailand. Encompassing a total of 27,469 km^2, this forest tract includes five protected areas totaling 7135 km^2 (Dinerstein et al., 1997). It thus offers the best chance for long-term viability of the tiger population in Malaysia, which is completely isolated from other continental tiger populations. Taman Negara also represents the only large forested land (>1000 km^2) in Peninsular Malaysia that comes under direct jurisdiction of the Department of Wildlife and National Parks, and thus the Federal Government. Furthermore, the largest tract of original lowland (<300 m ASL) forest is protected in the park. Taman Negara is the last stronghold for not only tigers but also many other endangered species in Malaysia. Yet, basic ecological information on the tiger–prey community in this significant conservation area is lacking. Thus, this study was initiated to provide baseline information on the status of tigers and their prey in the park.

Observations of tigers in rainforests are extremely rare. In addition to the inherent difficulty of observing cryptic, naturally low-density tigers, the nature of tropical forests hampers the direct observation, trapping, and radio tracking of rainforest tigers. The recent development of commercially available self-activating, remote-camera systems equipped with an infrared sensor has allowed researchers to look into the ecology of tigers in rainforest habitats (Franklin et al., 1999; Griffiths, 1994; Lynam et al., 2001; O'Brien et al., 2003). Karanth (1995) pioneered the use of camera trapping in the framework of mark-recapture theory (reviewed by Nichols, 1992) to estimate the tiger populations in India (Karanth and Nichols, 1998, 2000). We applied their method, but modified the sampling technique in order to estimate tiger densities at three sampling sites in Taman Negara. Photographic data in conjunction with track-count data were also used to estimate prey biomass and proportional occupancy of tigers and their prey species, and to assess potential human impacts on the predator–prey community. We tested three specific hypotheses: (1) tiger densities are positively correlated with prey biomass; (2) tiger densities in the primary rainforest of Malaysia are lower than those in grassland and deciduous forests of the Indian subcontinent; and (3) prey biomass and tiger density are depressed in areas with high levels of human traffic.

2. Methods

2.1. Study area

Taman Negara National Park (4°10′–4°56′N, 102°00′–103°00′E) is located in north-central Peninsular Malaysia (Fig. 1). Altitudes in the park range from 70 to 2187 m ASL at the peak of Mt. Tahan. Taman Negara receives an annual average of 2500 mm precipitation; rainfall is highest in November–February but there is no distinctive wet or dry seasons. Average relative humidity is 86% with little monthly variation from 82% minimum to 92% maximum. Temperatures also vary little with monthly maximum temperatures of 30–34 °C and monthly minimum temperatures of 22–23 °C (Malaysian Meteorological Service, in litt.). The forest type is broadly classified as a tropical evergreen moist forest, which ranges from lowland humid tropical forest to montane oak (Fagaceae) and ericaceous forests (Weber, 1972; Whitmore, 1984).

Based on logistics and accessibility, study sites were established at Merapoh (MP), Kuala Koh (KK), and Kuala Terengan (KT), which was about 8 km upstream from the park headquarters in Kuala Tahan (Fig. 1). General characteristics of the three sampling sites are summarized in Table 1. Merapoh offers the best accessibility by vehicle, it is only 8 km from the main road to the park entrance. A hard-surface road extends 13-km eastward into the park. This is the only road in the park, and it is used primarily to transport climbers closer to the peak of Mt. Tahan. At a road density of 0.023 km/100 km^2, this is one of the lowest in the world. The park's trail system is also limited, except for those leading to the peak of Mt. Tahan. Other trails are located near the four major tourist facilities, which are located at widely separated locations along the park

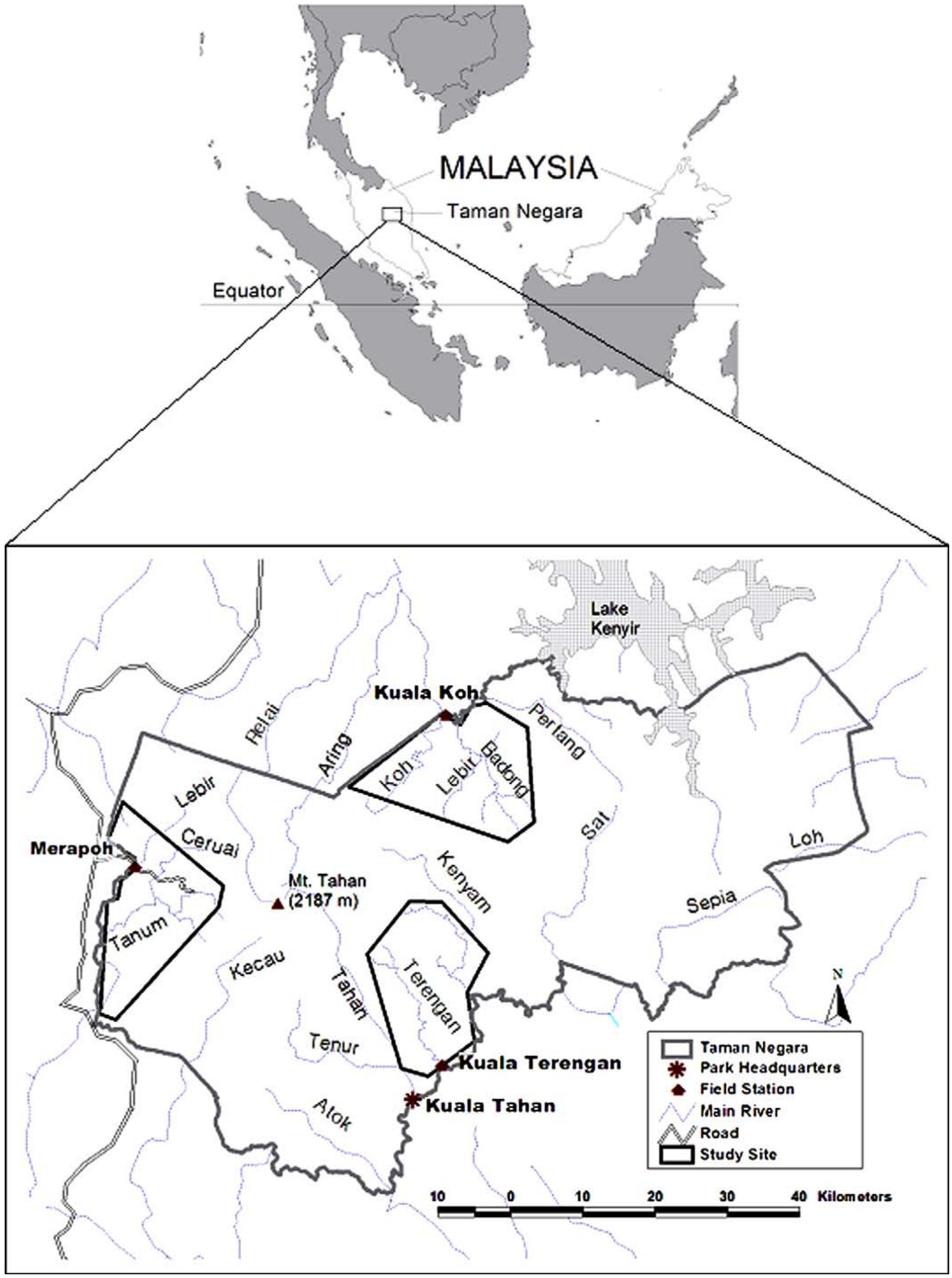

Fig. 1. Location of the three study sites, Merapoh, Kuala Terengan, and Kuala Koh in Taman Negara National Park in Peninsular Malaysia.

boundary. These logistic constraints have resulted in fewer field studies being conducted in Taman Negara than in other smaller and more accessible reserves in Malaysia (Marshall, 1973).

Besides tourists, the park is also used by approximately 400 Aborigines, locally called *Orang Asli*. The tribe of Aborigines living in the park is known as Batek. They are nomadic hunters and gatherers who sometimes engage in economic or commercial activities such as trading non-timber forest products or guiding tourists at Kuala Tahan. Batek's staple food source is tubers (yams) of the genus *Dioscorea* and fruits in season (van der Schot, 1990). Possession of firearms is prohibited and the Aborigines use blowpipes, poison arrows, smoke, and digging to obtain wild meat. The source of animal protein consists of small to medium-sized species such as primates, squirrels, birds, bird's eggs, porcupines, bamboo rats, pangolins, turtles, and fish. Large herbivores and carnivores are unaffected directly by the Batek's hunting techniques (van der Schot, 1990; Kawanishi,

Table 1
General characteristics of the three study sites in Taman Negara, Malaysia

	Study site		
	Merapoh	Kuala Terengan	Kuala Koh
Area sampled (km^2)	200	200	200
Vegetation	Lowland-hill dipterocarp	Lowland-hill dipterocarp	Lowland-hill dipterocarp
Elevation (m ASL)	90–714	70–706	70–898
Stream density index (%)[a]	100	100	100
No. of known salt licks	5	1	1
Road (km)	13	0	0
No. of annual visitors[b]	5257	55,673[c]	5528
Estimated no. Aborigines[d]	0	100–133	50–67

[a] Proportion of 1-km^2 grid with streams on 1:50,000 topographic maps. Some may be ephemeral during dry spell.
[b] Registered tourists in 2000 (Department of Wildlife and National Parks, Taman Negara, unpublished data).
[c] Registered tourists in Kuala Tahan, the park headquarter, 8 km downstream of Kuala Terengan. Exact number of tourists visited Kuala Terengan is unknown.
[d] van der Schot (1990) and personal observation, this study.

pers. observ.). Only 150–200 Batek appear to be full-time residents in the park. KT may support twice as many Batek as does KK (van der Schot, 1990, Kawanishi pers. observ. and interview with Batek). There are no Aborigines in MP. Therefore, combined with number of tourists (Table 1), the overall human traffic level was high at KT, medium at KK, and low at MP.

The land cover immediately outside the MP boundary is a mosaic of small secondary forests (<20 km^2), oil palm plantation, rubber plantation, and small orchards. Land cover outside the KT boundary is a large secondary forest (>5000 km^2), which was partly logged during the study period. There are also a few small villages (<1000 people) along the Temberling River, which is the major avenue of access to the park headquarters at Kuala Tahan. The land use pattern outside the KK boundary is a large-scale oil palm plantation and secondary forests that were partly logged during the study.

2.2. Field sampling

The general sampling design and statistical analyses follow Karanth and Nichols (1998, 2000) for estimation of tiger densities, O'Brien et al. (2003) for estimation of prey densities, and Nichols and Karanth (2002) for estimation of proportional occupancies. Necessary modifications and refinement made in the field sampling and analysis are described below and in Kawanishi (2002). Detailed specifications of two types of remote camera systems used in this study, TrailMaster® active infrared system (Goodson Associates, Inc., Kansas, USA) and CamTrakker® passive infrared system (CamTrak South, Inc., GA, USA), are in Kawanishi (2002).

The three sites – Merapoh (MP), Kuala Terengan (KT) and Kuala Koh (KK) – were sampled between April 1999 and May 2000, March 2000 and January 2001, and October 2000 and August 2001, respectively (Table 2). An area of approximately 200 km^2 was sampled at each site; a sample area of this size was judged sufficiently large to encompass the home range of several tigers. The goal of the camera trapping was to maximize the capture probabilities of tigers, and camera systems were placed at strategic locations beside active game trails with an average spacing of one unit every 4 km^2. Care was taken not to leave a sufficiently large area without camera traps where a tiger might have a zero capture probability. Trapping locations were by default stationary throughout the sampling period, but camera traps were occasionally moved to nearby areas with fresh tiger sign or shifted to a new location if preliminary results revealed poor animal traffic at the particular site. GPS coordinates of all trap locations were recorded and plotted on maps.

The major constraint in this study was limited mobility. Except for the 13-km-long road at MP, there are no roads in the park and it took 6–8 weeks of actual field time, sometimes stretching to over 3 months, just to "fill" the 200-km^2 sampling area with camera traps and to concurrently survey the area and check cameras set earlier. Consequently, each trap location was visited for maintenance and data retrieval only once a month. Due to the naturally low-densities and/or low capture probabilities of tigers in the sampling area, it took 10–13 months to accumulate the requisite data at each site (Table 2).

For individual identification both flanks of each tiger had to be photographed simultaneously. This was achieved by setting up two cameras, one opposite the other, at points along both sides of suspected tiger trails. Only photographs with clear individual identification were used for analysis. As a result, 3 of 38 tiger "detections" had to be discarded (Table 2).

In addition to photographic data, any secondary signs of all large predators (i.e., tigers, leopards *P. pardus*, and dholes *Cuon alpinus*) were recorded whenever encountered and large fecal samples (diameter >25 mm) were collected, dried and stored for analysis. Furthermore, 100-m-long transects in front of all camera traps

Table 2
Summary of sampling schedule, efforts and camera-trapping data on tigers collected at the three study sites in Taman Negara, Malaysia, 1999–2001

	Study site			
	Merapoh	Kuala Terengan	Kuala Koh	Total
Camera-trapping period	4/99–5/00	3/00–1/01	10/00–8/01	4/99–8/01
Days camera traps were operational	399	319	300	1018
Total trap-nights[a]	4336	4847	4871	14,054
No. of trap locations	47	43	45	135
Tiger photo[b]	22	14	25	61
Tiger detection[c]	12	11	15	38
Tiger capture[d]	11	9	15	35
Effective tiger capture[e]	8	7	12	27
No. of individual tigers captured, M_{t+1}	5	5	6	16
No. of trap-nights/tiger photo	197	346	195	230
No. of trap-nights/tiger detection	361	441	323	370
No. of trap-nights/tiger capture	394	539	323	402

[a] Total number of 24-h periods during which a camera trap was functional.
[b] Number of photographs of tigers excluding duplicates of the same individual taken simultaneously at a dual-camera setup.
[c] Total number of trap nights tigers were detected at each trap location.
[d] Total number of trap nights tigers with known identity were detected. The maximum number of capture of an individual tiger per night is one no matter how many times it is detected at other trap locations.
[e] Total number of tiger captures exclusive of those that occurred during the same sampling occasion.

and at random points between camera traps were surveyed monthly for animal tracks. The random points between camera traps changed monthly and only relatively fresh tracks (<1 month old) were recorded. Besides the human traffic recorded by camera traps and track-count surveys, evidence of human activities was recorded opportunistically to assess the potential human impacts on the tiger–prey community.

2.3. Data analysis

All statistical tests except for those in the program CAPTURE (see below) were performed using SPSS version 9.0.0 (SPSS, inc. Chicago, IL, USA) with the significance level of $P < 0.05$ unless noted otherwise.

2.3.1. Tiger density

Following the analytical procedure described by Karanth and Nichols (1998, 2000), the program CAPTURE (Otis et al., 1978; Rexstad and Burnham, 1991; White et al., 1982) was used to estimate the abundance of tigers at three study sites. The program estimates abundance of closed populations. Of seven possible models in CAPTURE, we used model M_h due to its robustness (Burnham and Overton, 1978; Otis et al., 1978). Model M_h assumes that each individual animal has unique capture probability that is unaffected either by the animal's response to traps or time. Since camera trapping is a non-invasive sampling method, we assumed that the sampling technique did not affect the survivorship or behavior of animals.

Capture histories were constructed for each tiger identified. A matrix consisted of i animals in rows and t trapping occasions in columns. Because tiger cubs were never photographed, i animals included only adult tigers. Although trapping effort varied considerably across trapping locations and over time all study sites showed a similar trend with 8–10 periodic cycles in cumulative daily trap nights that was largely due to the frequency of the monthly maintenance trip. We therefore used nine trapping occasions for all sites. The total trap-nights at each trapping location was divided by nine and capture history of i tigers were noted on each occasion. Capture histories were tallied from all the trapping locations at each sample site to construct the final capture matrix. Each trapping occasion ($n = 9$) consisted of an average of 520 trap-nights, about 12 nights per trap.

To estimate tiger densities, the abundance estimates based on CAPTURE were divided by effective trapping areas, $A(W)$, as follows:

$$\hat{D} = \frac{\hat{N}}{A(W)},$$

where $A(W)$ consisted of a buffer area of boundary width, W, surrounding the polygon enclosed by the outermost trapping locations (Karanth and Nichols, 1998). To estimate W, we used half the absolute maximum distance moved (AMDM) by tigers captured on more than one occasion at each site instead of mean maximum distance moved (MMDM) used by Karanth and Nichols (1998), which has the tendency to underestimate W when samples are small (Kawanishi, 2002). By using the AMDM instead of MMDM for W, $A(W)$ could not be estimated, but was treated as a known constant. Thus, for the associated variance of the density estimate, we used the variance estimated for the abundance in CAPTURE. This is likely to underestimate the variance of the density estimate, but we knew of no way to estimate a variance for AMDM.

2.3.2. Prey biomass

Forty-four large feces (diameter >25 mm), presumably from *Panthera* species, were collected opportunistically in the park. However, molecular analysis showed that only three scats were from tigers and four from leopards. Thus, we were not able to construct food habits of *Panthera* spp. nor could we analyze for prey selection. We therefore assumed primary prey species of tigers in Taman Negara were ungulate species weighing more than 2 kg, but excluded Asian elephants *Elephas maximus* and Sumatran rhinoceros. Whether tiger prey on tapir *Tapirus indicus* is an ongoing topic of discussion (Holden and Martyr, 1998; Kawanishi et al., 2002b), and it was initially included as a potential prey species. Limited data on kills and feces reveal that tigers preyed on sun bear *Helarctos malayanus* ($n = 3$), cattle calf *Bos taurus* ($n = 1$), and pangolin *Manis javanica* ($n = 1$). Other bear species, larger than sun bears, are reported as tiger prey elsewhere (Schaller, 1967). Thus, sun bear was included in the prey biomass estimate, but cattle and pangolin were not because the former almost never occur in the park (see Section 4) and photographs of the latter species were too few ($n = 6$) to be included in the biomass estimate calculation. In addition, common porcupines *Hystrix brachyura* were included because they weigh 8 kg on average (Medway, 1978) and were photographed frequently at all sites.

Photographic data were used to make a crude inference on available prey biomass. The analytical procedure for estimation of animal densities using program CAPTURE was applicable only for antlered male sambar deer *Cervus unicolor*. Capture histories were constructed for stags that were individually identifiable based on shape and color of antlers and mains. Growth and shedding of antlers over time were taken into consideration. For all other large herbivore species, we used a relative abundance index based on camera-trapping data to estimate densities. O'Brien et al. (2003) used density estimates from line transects for prey species and program CAPTURE for tigers to develop a regression analysis of the number of trap-nights required to photograph at least one individual conditional on species presence in the Bukit Barisan Selatan National Park in Sumatra.

To derive a density estimate for an ith species (D_i) at each study site, we used an average of linear and reduced major axis regressions presented in O'Brien et al. (2003). To mitigate possible undercounts of group-living species, the number of detections was multiplied by average group size (Table 3). Notations improvised for this study are as follows:

$$\hat{D}_i = \{\exp[(106.8 - \mathrm{RAI}_i)/59.8] + \exp[(111.4 - \mathrm{RAI}_i)/68.32]\})/2,$$

where relative abundance index for ith species (RAI_i) is

Table 3
Body weights and average group sizes used to estimate biomass of herbivores and potential prey species for tigers in Taman Negara, Malaysia

Species	Body weight (kg)	Group size
Common porcupine	8[a]	1.22[e]
Sun bear	56[b]	1.00[e]
Elephant	2088[c]	3.59[c]
Tapir	395[d]	1.00[e]
Wild boar	32[c]	2.23[c]
Mouse deer	3[a b]	1.00[e]
Sambar deer	134[c]	1.70[c]
Muntjac	21[c]	1.15[c]
Gaur	450[c]	6.99[c]
Serow	120[a]	1.00[e]

[a] Medway (1978).
[b] Payne et al. (1985).
[c] Karanth and Sunquist (1992).
[d] Khan (1997).
[e] This study, based on average number of individuals photographed at once in the same frame.

$$\mathrm{RAI}_i = \frac{\sum_j tn_j}{g_i \sum_j p_{ij}},$$

where tn_j is the total trap-nights at the jth trap location, g_i is an average group size for ith species and p_{ij} is a "detection" for ith species at jth trap location. A detection is more than one photograph of ith species at jth trap location taken during one trap-night. An untested assumption for this analysis was that the relationship between photographic data and independent density estimates was comparable between the studies conducted in Sumatra and Malaysia. Due to the untested assumption and no associated variances for the estimates, the inference made here is weak.

2.3.3. Proportion of occupancy

Proportion of each sample area occupied by tigers was estimated from observations of secondary sign and camera trapping data. Following the method described by Nichols and Karanth (2002), proportional occupancy was operationally defined as proportion of sampling units containing evidence of tiger activity, and was estimated as

$$\hat{\psi} = \frac{\hat{r}}{s},$$

where $\hat{\psi}$ is the estimated proportion of area occupied, $\hat{r}$ the estimated number of sampling units containing signs of tiger, and s is the total number of sampling units sampled. The variance for the estimated proportion of area occupied was estimated as

$$\hat{\mathrm{var}}(\hat{\psi}) \approx \frac{\hat{\mathrm{var}}(\hat{r})}{s^2} + \frac{\hat{\psi}(1-\hat{\psi})}{s}.$$

CAPTURE was used to estimate r. First, the sample area was subdivided into a 5 km × 5 km grid, or a

25 km^2 sampling unit. There were a total of nine such grids covering the entire sampling area in each site. Each grid was sampled with camera traps and monthly surveys for sign, including track-count sampling on 100-m transects. Data from five consecutive monthly sampling occasions were used to construct a capture matrix. The matrix consisted of columns of sampling occasions and the rows of grid cells, in which sign of tiger activities was found during the sampling occasions.

Because grids were sampled with different sampling intensity in terms of total number of camera-trap nights and area covered by surveys, an estimation based on the null model (M_0) with homogeneous capture probability would be inappropriate. Thus, high selection criterion for M_0, possibly due to limited sample size was ignored, and a model with the second highest criterion was used for estimation. This procedure was repeated to estimate the site occupancy of leopard, elephant, and gaur *Bos frontalis*. For other species, a 3 km × 3 km grid or a 9-km^2 sampling unit was used to better reflect the smaller home-range sizes of sun bear (Wong et al., in press), sambar deer (Zulfikar et al., 2001) and tapir (Williams, 1979). There was no home-range size information on wild boar *Sus scrofa* and muntjac *Muntiacus muntjac* from the local rainforest, but judging by the weight and average group size (Table 3) as well as the crude density estimate of these animals (this study), their home-range sizes were assumed similar to those of sambar deer and tapir rather than those of elephant and gaur. Because the majority of grids were sampled (25 out of 26 grids in MP, 24 out of 24 in KT, and 26 out of 28 in KK), random sampling was not necessary.

2.3.4. Activity patterns

The relation between predators and prey species in terms of activity patterns was investigated from the camera-trap data. When the camera is tripped, the time is imprinted on the photograph. The percent activity level was calculated based on pooled camera-trapping data from the three study sites, exclusive of photographs of the same species taken within one hour at the same trap location.

2.3.5. Potential human impacts

Level of human traffic was assessed by comparing indices based on camera-trapping (CPU = No. of detections per 100 trap nights) and track-count data ($RAI_{track\ count}$ = No. of transects/total transects surveyed). Spatial distribution of wildlife and humans in relation to park boundary (edge) and possible avoidance of humans by wildlife were examined using ArcView 3.1 (ESRI, Redlands, CA, USA) and correlation analysis based on CPU of species at each trap location. The level of significance was $P < 0.1$.

3. Results

3.1. Tiger density

A total of 4533 wildlife photographs, including mammals ($n = 4167$; Appendix A), birds ($n = 286$), reptiles ($n = 14$), and invertebrates ($n = 66$), was collected during 14,054 trap-nights between April 1999 and August 2001. Only 1.5% of the mammal photos were of tigers (Table 2). Over the course of study, camera trapping was successful in detecting all medium to large terrestrial mammals expected to occur in Taman Negara except for Sumatran rhino (Appendix A). A few rhino tracks were recorded in all study sites, indicating an extremely low-density species (Kawanishi et al., 2002a).

The long sampling period at each study site raised a concern for violation of the closure assumption. Although Otis et al. (1978) cautioned that the test statistic of CAPTURE has little chance of rejecting closure in the case of small samples, at least no marked departure from the assumption was suggested by the test result (Table 4). The estimated probabilities that a tiger was captured on a single sampling occasion were consistent across the three sites and the estimated probabilities that

Table 4
Estimated abundance of tigers and other relevant statistics for mark-recapture analysis of tigers sampled at the three study sites, Merapoh, Kuala Terengan, and Kuala Koh in Taman Negara, Malaysia from 1999 to 2001

		Study site		
		Merapoh	Kuala Terengan	Kuala Koh
No. of occasion	T	9	9	9
Closure test	P	0.19	0.94	0.073
Selection criteria	M_o	1.00	0.92	0.98
	M_h	0.86	1.00	1.00
No. of animals captured	M_{t+1}	5	5	6
Estimated average capture probability per sampling occasion	$\hat{\bar{p}}$	0.13	0.16	0.22
Estimated capture probability over all sampling occasion	$M_{t+1}/\hat{N}$	0.71	1.00	1.00
Population estimate and standard error	$\hat{N}(SE[\hat{N}])$	7 (1.92)	5 (2.35)	6 (2.44)
95% confidence interval of estimate	95% CI	6–14	5–20	6–21
Coefficient of variation	CV (%)	27.4	47.0	40.7

Table 5
Mean maximum distance moved by photographically recaptured tigers, effective sampling areas, and estimated tiger density at the three study sites in Taman Negara, Malaysia, 1999–2001

	Study site		
	Merapoh	Kuala Terengan	Kuala Koh
Area with camera traps (km^2)	165.47	164.20	151.41
Absolute maximum distance moved (km)	6.05	8.22	5.17
Boundary width (km)	3.03	4.11	2.59
Effective sampling areas (km^2)	353.60	452.50	317.24
Estimated tiger density and standard error (no./100 km^2)	1.98 (0.54)	1.10 (0.52)	1.89 (0.77)
95% Confidence Interval	1.70–3.96	1.10–4.42	1.89–6.62

Table 6
Density and biomass estimates of herbivores and potential tiger prey in the three study sites in Taman Negara, Malaysia, 1999–2001

	Study site					
	Merapoh		Kuala Terengan		Kuala Koh	
	Density (/km^2)	Biomass (kg/km^2)	Density (/km^2)	Biomass (kg/km^2)	Density (/km^2)	Biomass (kg/km^2)
Common porcupine	1.46	12	0.33	3	1.02	8
Sun bear	1.57	88	1.13	63	1.45	81
Wild boar	4.17	133	3.63	116	4.62	148
Mouse deer	0.37	1	0.83	2	0.62	2
Sambar deer	0.20	27	0.01	1	3.22 (0.16)[a]	431 (21)[a]
Muntjac	3.20	67	3.26	68	4.05	85
Gaur	0.22	98	0.03	11	0.00	0
Serow	0.00	0	0.00	0	0.23 (0.006)[a]	28 (<1)[a]
Elephant	3.56	7428	0.81	1684	2.10	4382
Tapir	3.76	1484	1.32	520	2.36	933
Total	18.51	9337	11.35	2469	16.39	5661
Total – elephant	14.95	1909	10.54	785	14.29	1279
Total – elephant – tapir	11.19	426	9.22	266	11.93	346

[a] Densities and corresponding biomass of sambar deer and serow in Kuala Koh were clearly overestimated, using the calibration method presented in O'Brien et al. (2003). Adjusted estimates are in parenthesis. The total biomass in Kuala Koh is based on the adjusted biomass. See text for explanation and method used for the adjustment.

a tiger was captured at least once over the sampling period were high at all sites. Estimates of tiger population sizes at MP, KT, and KK were seven, five and six animals, respectively (Table 4).

The estimated tiger densities varied between 1.10 and 1.98 tigers/100 km^2 (Table 5). The hypothesis that the three samples came from one population was tested using program CONTRAST (Hines and Sauer, 1989). The differences were not significant ($X^2 = 1.56$, df = 2, $P = 0.46$) with the overall mean of 1.66 ± 0.21 (SE) tigers/100 km^2.

3.2. Prey biomass

There was a strong positive correlation between the photographic data and track-count data of large mammals (Appendix A) at all the sites (MP: $r = 0.67$, $P = 0.001$; KT: $r = 0.76$, $P < 0.0005$; KK: $r = 0.85$, $P < 0.0005$), suggesting that these data could provide indices for relative abundance. There were unusually high numbers of photographs of sambar deer and serow *Naemorhedus sumatrensis* in KK resulting in relatively high density estimates (Table 6). All serow photos ($n = 43$, compared to one and eight for other study sites; Appendix A) of two animals came from a single trapping location. Monthly track surveys confirmed that serow was unlikely to be present at other areas in the study site. Thus serow density was adjusted using two animals in the effective trapping area of 317.24 km^2. Similarly, a large proportion of the sambar deer photos (86% of a total $n = 293$; Appendix A) came from two trap locations at the only salt lick in the study site. Using program CAPTURE, the population estimate under model M_h for male sambar deer with antlers was 15 ± 3.18 (SE) animals with the estimated average capture probability of 0.14. Using a ratio of 3:7 for adult and yearling males to all others (Karanth and Sunquist, 1992), an estimate of 50 sambar deer was reached. Therefore, the density estimate in the study site was adjusted to 0.16 animals/km^2 in contrast to the original 3.22 animals/km^2. Using CAPTURE to estimate sambar deer abundance was not applicable to other study sites

Table 7
Estimated proportion of area occupied by large mammal species based on monthly surveys of secondary signs and camera-trapping data collected for five months each at the three study sites in Taman Negara, Malaysia, 1999–2001

Grid size (km^2)	Tiger	Leopard	Bear	Muntjac	Pig	Sambar Deer	Gaur	Elephant	Tapir
	25	25	9	9	9	9	25	25	9
Merapoh									
M_{t+1}[a]	5	7	13	23	19	9	5	8	19
Model used	M_h	M_h	M_h	M_b	M_h	M_{th}	M_h	M_{th}	M_b
$\hat{r}(SE[\hat{r}])$[b]	6 (1.2)	9 (1.8)	17 (3.2)	25 (3.9)	22 (3.0)	16 (7.7)	6 (1.2)	9 (2.4)	19 (0.1)
$\hat{\psi}(\mathrm{var}[\hat{\psi}])$[c]	0.67 (0.044)	1.00 (0.038)	0.68 (0.025)	1.00 (0.025)	0.88 (0.019)	0.64 (0.104)	0.67 (0.043)	1.00 (0.068)	0.76 (0.007)
Kuala Terengan									
M_{t+1}	6	5	12	24	24	10	6	9	16
Model used	M_h	M_{th}	M_b	M_{th}	M_h	M_h	M_h	M_{th}	M_{th}
$\hat{r}(SE[\hat{r}])$	7 (1.2)	7 (3.0)	12 (0.1)	24 (1.4)	24 (2.6)	11 (2.5)	9 (5.0)	9 (2.9)	17 (2.1)
$\hat{\psi}(\mathrm{var}[\hat{\psi}])$	0.78 (0.038)	0.78 (0.131)	0.50 (0.010)	1.00 (0.004)	1.00 (0.011)	0.46* (0.021)	1.00 (0.309)	1.00 (0.104)	0.71* (0.016)
Kuala Koh									
M_{t+1}	7	6	16	26	26	17	1	7	22
Model used	M_h	M_h	M_h	M_h	M_h	M_h	na[d]	M_{th}	M_h
$\hat{r}(SE[\hat{r}])$	7 (2.3)	9 (5.5)	18 (3.0)	26 (2.7)	26 (3.1)	21 (4.0)	na	7 (0.7)	26 (4.7)
$\hat{\psi}(\mathrm{var}[\hat{\psi}])$	0.78 (0.083)	1.00 (0.371)	0.69 (0.022)	1.00 (0.011)	1.00 (0.014)	0.81 (0.029)	0.11	0.78 (0.026)	1.00 (0.033)

[a] Number of grid cells at which any given species was photographed or detected by signs.
[b] Estimated number of grid cells at which signs of any given species were present and standard error of the estimate.
[c] Estimated proportion of the area occupied by any given species and variance of the estimate.
[d] Presence of gaur was documented only once in one grid, thus no model was available to estimate the site occupancy. The point estimate without variance was based on one out of nine grids containing gaur signs, thus 0.11.
* Ungulate species with proportion of occupancy significantly lower at $P < 0.05$ than 100% occupancy of muntjac in the area.

due to limited captures ($n = 3$ for stags in MP; $n = 2$ in KT). The total biomass of serow and sambar in KK was thus based on these two adjusted estimates.

Total biomass estimates of large herbivores at the three study sites ranged from 2469 to 9337 kg/km^2, depending largely on density estimates of elephant (Table 6). On average, two of the mega-herbivores, elephant and tapir, contributed 94% of the wild herbivore biomass in the area. Elephant alone contributed about 77% of the biomass. Estimates of available prey biomass increased considerably (300–450%) if tapirs were included as prey (Table 6). The biomass estimate was the highest in MP where the tiger density estimate was also the highest. The positive relationship between the prey biomass and tiger densities generally conformed to our a priori expectation. However, the statistical power to test the hypothesis was weak due to the weak inference with no associated variance on the estimated prey biomass.

3.3. Proportion of occupancy

Estimated proportion of area occupied by leopards was equal or slightly higher than that of tigers (Table 7), but the difference was not significant at any of the sites (MP: $X^2 = 1.36$, df = 1, $P = 0.24$; KT: $X^2 = 1.0$, df = 2, $P = 1.0$; KK: $X^2 = 0.11$, df = 1, $P = 0.75$). Proportional occupancy of each species was relatively consistent across sites (tigers: $X^2 = 0.17$, df = 2, $P = 0.92$; leopards: $X^2 = 0.30$, df = 2, $P = 0.86$). Among ungulates, the highest occupancy rates were attained by muntjac at 100% in all sites, followed by wild boar ranging from 88% to 100%. Elephants and tapirs also had high proportions of occupancy, at 71–100% and 78–100%, respectively. Sambar deer and gaur had relatively lower occupancies compared to other ungulate species. Gaur were rare in KK with only one record found during the sampling period (Table 7).

3.4. Activity patterns

Tigers and leopards were more diurnal than nocturnal and there was considerable overlap between species (Fig. 2a). Dhole were excluded from this analysis due to limited sample size ($n = 9$), but all dhole captures were registered between 0800 and 1900 h. The activity patterns of the *Panthera* species were more similar to those of crepuscular/diurnal species such as muntjac, mouse deer *Tragulus* spp., and pig (Fig. 2(b)) than to nocturnal species such as tapir and sambar deer (Fig. 2(c)). Sample sizes for tiger, leopard, muntjac, mouse deer, pig, tapir, and sambar deer were 43, 140, 475, 94, 401, 376 and 179 activity records, respectively.

3.5. Potential human impacts

Of 854 photographs of humans taken at all study sites, no person was carrying a firearm or animal carcasses. Of 160 signs of human activities encountered

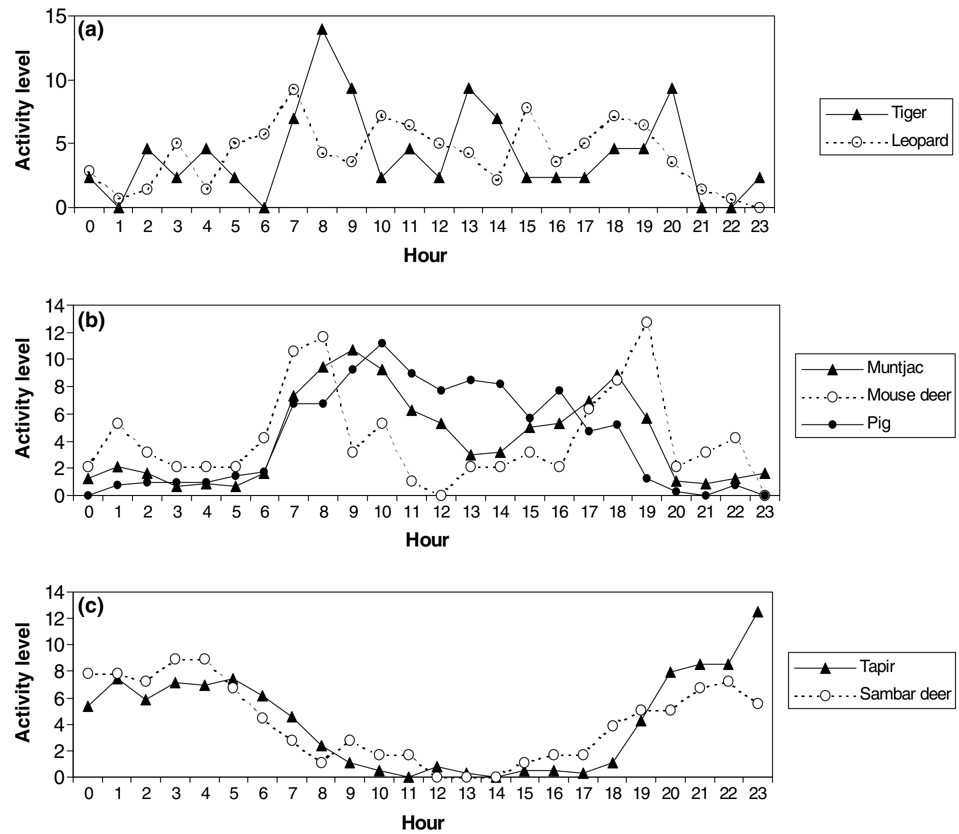

Fig. 2. Activity levels (%) of tigers and leopards (a), and their potential prey species (b) crepuscular/diurnal species and (c) nocturnal species, based on pooled camera-trapping data from the three study sites in Taman Negara, Malaysia, 1999–2001.

(excluding footprints and cut vegetation smaller than saplings), we found no evidence of poaching of large mammals. There were no animal remains at investigated campsites ($n = 63$). No traps, snares, or empty cartridges were recovered and no gun shots were heard in the study sites.

The $RAI_{track\ count}$ for humans was 0.025, 0.117 and 0.148 for MP, KK and KT, respectively. Likewise, the CPU based on camera-trapping data were 0.6, 2.0 and 2.4, respectively. Both indices correlated positively with the different level of human traffic by both tourists and Aborigines (Table 1). It was generally observed that prey biomass and tiger density estimates were lowest in KT, where human traffic level was highest. Furthermore, occupancy rates of sambar and tapir were lower in KT compared to muntjac (sambar: $X^2 = 12.37$, df = 1, $P = 0.0004$; tapir: $X^2 = 4.03$, $P = 0.045$; Table 7).

Human CPU was higher at trap locations closer to the park boundary, especially within 6 km, a distance that can be traveled in half a day, to the park boundary (MP: $r = -0.26$, $P = 0.09$; KT: $r = -0.28$, $P = 0.07$; KK: $r = -0.35$, $P = 0.01$). Besides humans, wild boar in MP ($r = -0.39$, $P = 0.01$) responded positively to edges while muntjac ($r = 0.26$, $P = 0.07$) and elephant ($r = 0.40$, $P = 0.004$) showed negative responses to the edge in KK. Human CPU showed no correlation with distance to the road in MP ($r = -0.19$, $P = 0.23$) nor distance to salt lick sites (MP: $r = -0.04$, $P = 0.77$; KT: $r = -0.26$, $P = 0.10$; KK: $r = -0.14$, $P = 0.32$). No species except for muntjac in KT ($r = -0.29$, $P = 0.06$) showed any association to human CPU.

4. Discussion

The camera-trapping sampling technique in the mark-recapture framework was successful in providing the first statistically valid model-based density estimates of tigers in the lowland rainforest of Malaysia. Efforts required to collect requisite data were, however, large with an average of 4685 trap-nights over 11 months per site, which is impractical to recommend for most applications. That the estimates permitted only a weak inference was an inevitable consequence of the small samples. Abundance estimation of prey species was even more problematic because the mark-recapture models were not applicable. Due to the lack of data from local forests (i.e., independent density estimates, average weight and group size), the inference on the prey biomass was admittedly even weaker with no associated variance for the estimate. Nevertheless, these weak inferences were still better than traditional "guesstimates" based on the unrealistic assumption of total and simultaneous counts of tracks that are identified to individual animals.

4.1. Tiger population in Taman Negara

Based on density estimates, an attempt was made to estimate the tiger population in the entire park. Although the sampling sites were not randomly selected, results suggested that the samples were taken from one population that occupied the area. In addition, the total effective trapping area constituted approximately 30% of lowland to hill forest of Taman Negara. Furthermore, inventory surveys conducted by the Department of Wildlife and National Parks in 2001 and 2002 found sign of tigers in all major tributaries in the park (DWNP, in litt.). For these reasons, we assume that the sample population was a good representation of the population in the lowland to hill forest of Taman Negara. The highest elevation in all the study sites was 898 m. Therefore the mean density estimate of 1.66 ± 0.21 tigers/100 km^2 was extrapolated to the area below 900 m, which constituted 89.7% of the park. Thus, 90% of Taman Negara supported an estimated 65 (95% CI: 49–81) adult tigers. A further attempt was made to include areas above 900 m and cubs into the total population estimate. In a primary rainforest of Sumatra, Griffiths (1994) reported that tiger density in montane forest above 1700 m was about half of that of lowland forest below 600 m. A demographic model of wild tiger populations suggests that cubs may form ~25% of a 'normal' tiger population (Karanth and Stith, 1999). Assuming that tigers existed above 900 m at a reduced density of 0.83 tiger/100 km^2, and that 25% of the population consisted of cubs, the entire park could support 91 (95% CI: 70–112) tigers.

4.2. Tiger density and prey biomass in rainforests

Animal density is a function of habitat productivity, metabolic needs of the species and size of the area. As such, home range sizes of breeding tigresses are strongly correlated with large ungulate prey (Sunquist, 1981). There is a clear relation between prey biomass and tiger density across the tiger's range (Fig. 3; $R^2 = 0.78$, $P < 0.0001$). Primary rainforests offer little primary productivity at ground level, and thus mammalian biomass is dominated by arboreal herbivores (Eisenberg, 1980). Consequently, tropical rainforest is not particularly good habitat for tigers as it does not support a diversity or abundance of large terrestrial ungulates. The estimated tiger densities in the primary rainforest of Malaysia are, as predicted, among the lowest densities recorded in the entire range (Fig. 3).

There are two other reliable estimates of tiger density from primary rainforests. Using estimated home-range

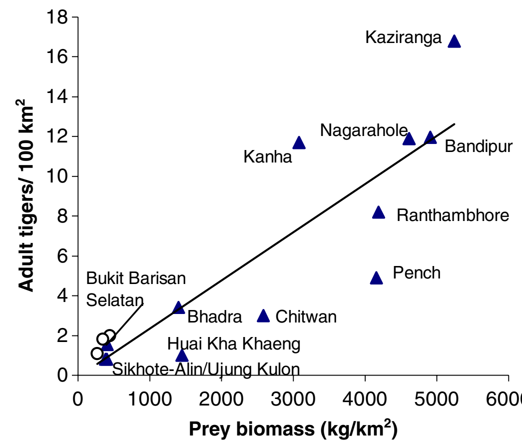

Fig. 3. The significant relation between prey biomass and adult tiger density across tiger range ($R^2 = 0.78$, $P < 0.0001$). The three empty circles represent the data points from this study. Sikhote-Alin (Russia) and Ujung Kulon (Java) have graphically overlapping points. Data source: Karanth and Nichols (2000) for Kaziranga, Bandipur, Nagarahole, Kanha, Ranthambhore, Bhadra, and Pench; Sunquist (1981), Eisenberg and Seidensticker (1976) for Chitwan; Rabinowitz (1989), Srikosamatara (1993) for Huai Kha Khaeng; O'Brien et al. (2003) for Bukit Barisan Selatan: Miquelle et al. (1999) for Sikhote-Alin; and Hoogerwerf (1970) for Udjung Kulon.

size based on camera-trapping data and observations of tracks, Griffiths (1994) calculated the tiger density in the primary lowland forest (<600 m) of the Gunung Leuser National Park (GLNP) in northern Sumatra to be 1.65 tigers/100 km^2. Another estimate based on camera-trapping data using CAPTURE was 1.56 ± 0.43 tigers/100 km^2 in a lowland forest (<500 m) of Bukit Barisan Selatan National Park (BBSNP) in southern Sumatra (O'Brien et al., 2003). The overall mean density estimate of 1.66 ± 0.21 tigers/100 km^2 of this study is similar to both of these estimates. It thus seems reasonable to conclude that a large tract of lowland to hill primary rainforest supports about 1.6 tigers/100 km^2. This conforms to another report from Sumatra that tiger densities in lowland forests are generally 1–3 tigers/100 km^2 (Santiapillai and Ramono, 1987). The higher end of this generalization applies to more productive lowland mixed grassland–forest and secondary forests rainforest such as Way Kambas National Park rather than primary forest. The tiger density in Way Kambas was estimated to be 1.6–4.3 tigers/100 km^2 (Franklin et al., 1999).

Based on the average density estimates of large herbivores, excluding elephants, tapirs, and Sumatran rhinoceros (Table 2 in O'Brien et al., 2003), we calculated the estimated prey biomass of the primary rainforest of Sumatra's BBSNP to be 408 kg/km^2. This was comparable to the biomass estimates, excluding the same three mega-herbivore species, at the three sites in Taman Negara, which ranged from 266 to 426 kg/km^2. There was no difference in the tiger densities between the two sites ($X^2 = 0.05$, df = 1, $P = 0.82$) despite the fact that BBSNP is subjected to heavy poaching of tigers (>8 tigers/year) and prey (O'Brien et al., 2003). Some evidence suggests that poaching rate of tigers in GLNP in northern Sumatra is equally high (Griffiths, 1994), whereas there were no records of poaching for Taman Negara. The high poaching rates in Sumatra may be sustained in the short run by the high recruitment of surviving tigers because both BBSNP (3568 km^2) and GLNP (8000 km^2) are large enough to support more than 40 adult tigers (Griffiths, 1994; O'Brien et al., 2003).

Until recently only three prey biomass estimates were available for tigers from tropical evergreen forests, all from Indonesia (Hoogerwerf, 1970; Borner, 1978 in Seidensticker, 1986; Seidensticker and Suyono, 1980). These crude estimates ranged from 200 to 400 kg/km^2, which led Seidensticker (1986) to conclude that the biomass of essential ungulate prey species for tigers in Asian rainforests does not exceed 500 kg/km^2. Although the method to estimate the prey biomass in this study was crude and the underlying assumptions untested, the result was as expected of a typical primary rainforest.

It is likely that Taman Negara tigers occasionally supplement their diet with livestock taken outside the park. However, livestock do not appear to constitute a primary prey for tigers in Taman Negara because: (1) <10% of the park's boundary is adjacent to agricultural lands where livestock occur (Department of Agriculture, 1992); (2) there is limited grazing opportunity in the primary rainforest and the wide rivers that form part of the park boundary effectively keep livestock outside the park; and (3) the one fecal sample containing cow was collected on the road in MP, which extended to an adjacent oil palm plantation where free-roaming cattle were available. Nevertheless, during the 19 months spent in MP, there was no depredation case reported to DWNP or police. The fecal sample in question was collected by DWNP staff after we moved to KT.

4.3. Tiger–prey relationship

Based on food consumption and weight of large cats (*Panthera tigris*, *P. leo*, *P. onca*, and *Puma concolor*), Emmons (1987) estimated daily food consumption of large cats to be 34–43 g/day/kg. By applying these values to the estimated weights of Malay tigers (i.e., 100 kg for females and 120 kg for males), the estimated annual consumption of female and male tigers is 1241–1570 and 1490–1883 kg, respectively. Adding 30% inedible parts of prey to the respective totals, female and male tigers need to kill 1613–2041 and 1936–2448 kg of prey annually for maintenance.

The estimated potential prey biomass available within the effective sampling areas in MP, KT and KK were 150,634 kg, 120,356 kg and 109,765 kg, respectively. Assuming a male to female sex ratio of 1:3, which appears typical of tiger populations, the prey biomass needed to support the estimated population of tigers annually was 11,856–14,999 kg in MP, 8469–10,714 kg in KT and 10,163–12,857 kg in KK. The estimated cropping rates by tigers at the corresponding study sites were therefore 7.9–10.0%, 7.0–8.9% and 9.3–11.7%, respectively. The actual cropping rate may be higher if other large predators (i.e., leopard and dhole) were included. However, the estimated prey biomass for tigers did not include smaller and more diverse prey species that are often taken by leopards (Seidensticker, 1976; Bothma and LeRiche, 1986; Rabinowitz, 1989; Sunquist, 1981; see Sunquist and Sunquist, 1989 for review). These may include arboreal/scansorial species (e.g., primates, giant squirrels, civets, and mongooses) and smaller species (e.g., pangolins, moonrats, bamboo rats, birds and lizards). Also, because dhole were rare in the park (CPU: 0.04–0.10), the prey biomass collectively removed by all three predators was undoubtedly higher than estimated for tigers alone, but the overall cropping rate may not be too different from estimated.

The estimated cropping rates from Taman Negara are comparable to those reported for tigers and leopards in Chitwan, Nepal at 8–10% (Sunquist, 1981), jaguars and pumas in Manu, Peru at 8% (Emmons, 1987), and all the large predators in Serengeti, East Africa at 9–10% (Schaller, 1972). If tapir are included as prey, the estimated cropping rates in Taman Negara decline to 1.8–3.2%. These rates are considerably lower than expected, suggesting that tapir are probably not a primary prey for tigers. Tapir are, however, both abundant (Table 6) and widely distributed (Table 7), suggesting that tigers may be avoiding tapir for reasons that are unknown.

Considering wild boar abundance, biomass (Table 6), occupancy (Table 7), and their high reproductive rate (Diong, 1973), pigs are the most important potential prey species, followed by muntjac. They are both protected game species under the Wildlife Protection Act of 1972, meaning they can be hunted with license outside protected areas. Wild boar are not consumed by the majority of Malaysia who are Muslims while muntjac is the most sought after bush meat.

4.4. Potential human impacts

Taman Negara is not a pristine untouched forest. Albeit low density, it has had human inhabitants dependent on natural resources for daily survival for at least 3000 years (Nicholas, 2000). A negative correlation between level of human traffic and abundance of large mammals was observed, but overall impacts on the tiger–prey community appear to be minimal in Taman Negara because: (1) we found no evidence of poaching of tigers or prey, (2) the primitive hunting techniques of Aborigines appear to have little effect on large mammals, (3) the Aborigine density in the park is extremely low at 0.046 individuals/km^2 and their range of activity does not cover the entire park, (4) areas affected by tourists are limited to small areas near park boundary, (5) the road access into the park is limited except in MP, and (6) about 90% of the park boundary is adjacent to forests (Department of Agriculture, 1992; Department of Forestry, in litt.). In addition, the low human traffic and the landuse pattern outside MP, coupled with the number of salt licks in the area, probably contributed to the abundance of wildlife in that area. That large mammals generally did not avoid human nor park boundary and that large predators were active during

Table 8

Common name	Scientific name	MP		KT		KK	
		Photo[a]	Track[b]	Photo	Track	Photo	Track
Tree shrew	*Tupaia* spp.[c]	0	0	4	0	0	0
Bat	*Chiropteran* spp.[c]	3	0	3	0	2	0
Pig-tailed macaque	*Macaca nemestrina*	11	0	3	0	26	1
Long-tailed macaque	*Macaca fascicularis*	1	0	0[#s]	0[#s]	0	0
Dusky langur	*Trachypithecus obscurus*	0[#sv]	0[#sv]	0[#sv]	0[#sv]	1	0
Banded langur	*Presbytis femoralis*	0[#sv]	0[#sv]	0[#sv]	0[#sv]	0[#sv]	0[#sv]
White-handed gibbon	*Hylobates lar*	0[#sv]	0[#sv]	0[#sv]	0[#sv]	0[#sv]	0[#sv]
Black siamang	*Hylobates syndactylus*	0[#sv]	0[#sv]	0[#sv]	0[#sv]	0[#sv]	0[#sv]
Pangolin	*Manis javanica*	3	0	2	1	1	0
Squirrel	*Sciurid* spp.[c]	3	0	1	0	0[#s]	0[#s]
Three-striped ground squirrel	*Lariscuc insignis*	0	0	1	0	0	0
Shrew-faced squirrel	*Rhinosciurus laticaudatus*	1	0	0	0	0	0
Spiny rat	*Maxomys* spp.[c]	1	0	4	0	0	0
Long-tailed giant rat	*Leopoldamys sabanus*	0	0	2	0	0	0
Common porcupine	*Hystrix brachyura*	56	8	27	4	42	17
Brush-tailed porcupine	*Atherurus macrourus*	6	0	17	0	0	0
Dhole (wild dog)	*Cuon alpinus*	6	2	2	0	8	5
Sun bear	*Helarctos malayanus*	96	8	66	18	63	30
Yellow-throated marten	*Martes flavigula*	5	0	0	0	2	0
Malay weasel	*Mastera nudipes*	0[#s]	0[#s]	0	0	0	0
Otter	*Lutra* spp.[c]	0[#s]	0[#s]	0[#s]	0[#s]	1	5
Malay civet	*Viverra tangalunga*	61	1	5	0	15	1
Masked palm civet	*Paguma larvata*	0	0	1	0	5	0
Common palm civet	*Paraduxurus hermaphroditus*	1	0	1	0	2	0
Large indian civet	*Viverra zibetha*	2	0	0	0	5	0
Binturong	*Arctictis binturong*	1	0	0	0	2	0
Banded palm civet	*Hemigalus derbyanus*	1	0	4	0	0	0
Banded linsang	*Prionodon linsang*	0	0	1	0	0	0
Tiger	*Panthera tigris*	22	0	14	6	25	14
Leopard	*Panthera pardus*	113	4	24	0	13	3
Clouded leopard	*Neofelis nebulosa*	5	2	6	0	5	1
Golden cat	*Catopuma temminckii*	21	0	4	0	12	0
Marbled cat	*Pardofelis marmorata*	1	0	5	0	10	0
Leopard cat	*Prionailurus bengalensis*	59	2	1	1	2	12
Elephant	*Elephas maximus*	167	49	43	57	80	86
Sumatran rhinoceros	*Dicerorhinus sumatrensis*	0[#t]	0[#t]	0	2	0	1
Tapir	*Tapirus indicus*	317	42	78	61	137	103
Pig (Wild boar)	*Sus scrofa*	132	80	117	151	256	220
Mouse deer	*Tragulus* spp.[c,d]	28	17	67	30	36	31
Sambar deer	*Cervus unicolor*	20	16	7	38	293	106
Muntjac	*Muntiacus muntjac*	138	49	155	105	262	103
Gaur	*Bos frontalis*	5	28	4	24	0	2
Serow	*Naemorhedus sumatrensis*	1	0	8	17	43	4
Human	*Homo sapiens*	49	3	467	43	338	36
Mammal total		1336	311	1144	558	1687	781
Total effort[e]		4336	119	4847	291	4871	308

[#] Species that was neither camera trapped nor recorded during track-count surveys, but the presence was confirmed in the study site by sighting (#s), vocalization (#v), or tracks recorded outside the track-count surveys (#t).

[a] Total number of photographs.

[b] Total number of 100-m transects on which tracks were observed.

[c] Animals appeared too small on photographs to be identified to the species level.

[d] Two species of the mouse deer, *Tragulus napu* and *T. javanicus*, were pooled as they were sometimes indistinguishable on photographs.

[e] Total trap-nights for camera-trapping data and total number of transects sampled for track data.

day when tourists and Aborigines were active were the testaments of minimal human impacts in the study sites.

The lack of poaching pressure on large mammals found in this study was supported for other parts of the park during the same period (Taman Negara Superintendent, in litt.), suggesting that the anti-poaching activities by DWNP in cooperation with the Police and Military were effective. A possible threat to tigers in Taman Negara and other forests throughout Malaysia is people from neighboring Thailand who illegally collect non-timber forest products (Abdul Kadir, 1998; Barden et al., 2000; Wan Shahruddin, 1998). Because there was ample evidence of the presence of Thais in the park (DWNP, in litt.; Kawanishi, 2002) and some Thais carry snares (IRF, 2002; Wan Shahruddin, 1998), the efforts to remove them from Taman Negara must continue to ensure the resilience of this large park to absorb the negative but legal human impacts exerted on selected boundary areas.

5. Conservation implications

Other things being equal, smaller populations are more prone to extinction (MacArthur and Wilson, 1967). Rainforest tigers are particularly vulnerable because they occur at lower densities than tigers elsewhere except for the Russian Far East (Fig. 3). Demographic parameters of wild Malay tigers are unknown. If they are similar to those of tigers studied elsewhere, population viability analyses predict that a "typical" tiger population of at least 68 adult animals or 24 breeding females has a high probability of persistence over the next 100 years if there is little poaching of tigers and prey, while ignoring possible effects of habitat loss, disease, and environmental catastrophes (Karanth and Stith, 1999; Tilson et al., 1994). The findings of this study suggest that the Taman Negara tiger population may meet the condition.

It is however unwise to be complacent even when the anti-poaching effort appears successful because a slight increase in poaching can greatly increase the probability of extinction (Kenney et al., 1995; Karanth and Stith, 1999). Furthermore, demographic and genetic consequences of poaching might not be immediately obvious and extinction could occur many years after poaching is reduced (Kenney et al., 1995). Therefore, the current anti-poaching patrol must be continued and the trend in abundance of both tigers and prey species needs to be closely monitored using the sampling-based methods. This study provides the benchmark figures using reliable and repeatable techniques. Specific limitations and possible improvements of the technique are discussed in Kawanishi (2002).

Currently, Malay tigers are distributed widely but sparsely throughout the forests of the peninsula (DWNP, in litt.). Because a large proportion of the forest coverage in Peninsular Malaysia is in forest reserves (35% of the total land cover) rather than protected areas (6%), the conservation status of tigers in most parts is not assured. Tigers and other wildlife are best protected in Taman Negara due to its vastness, remoteness, legislation, anti-poaching patrols, controlled legal activities at selected small areas, and low human and road densities. Taman Negara is set in a larger and more complex cultural and environmental landscape. The long-term viability of Taman Negara's tiger population needs to be evaluated as part of the large–scale tiger–prey–human communities in the surrounding forests. Together, these large clusters of forests, small agriculture holdings, and remote villages form the Greater Taman Negara Landscape of 15,000 km^2 where the largest contiguous tiger population in Indochina may occur. The cooperation among the Wildlife Department, Forestry Department and state development agencies is necessary to expand the research initiative, monitoring of tiger and prey populations and on-the-ground patrol in Taman Negara into the Greater Taman Negara Landscape.

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Appendix A

Mammalian species detected with camera traps or recorded during monthly track-count surveys in the three study sites, Merapoh (MP), Kuala Terengan (KT), and Kuala Koh (KK) in Taman Negara National Park, 1999–2001, see Table 8.

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