Cryptic mammals caught on camera: Assessing the utility of range wide camera trap data for conserving the endangered Asian tapir

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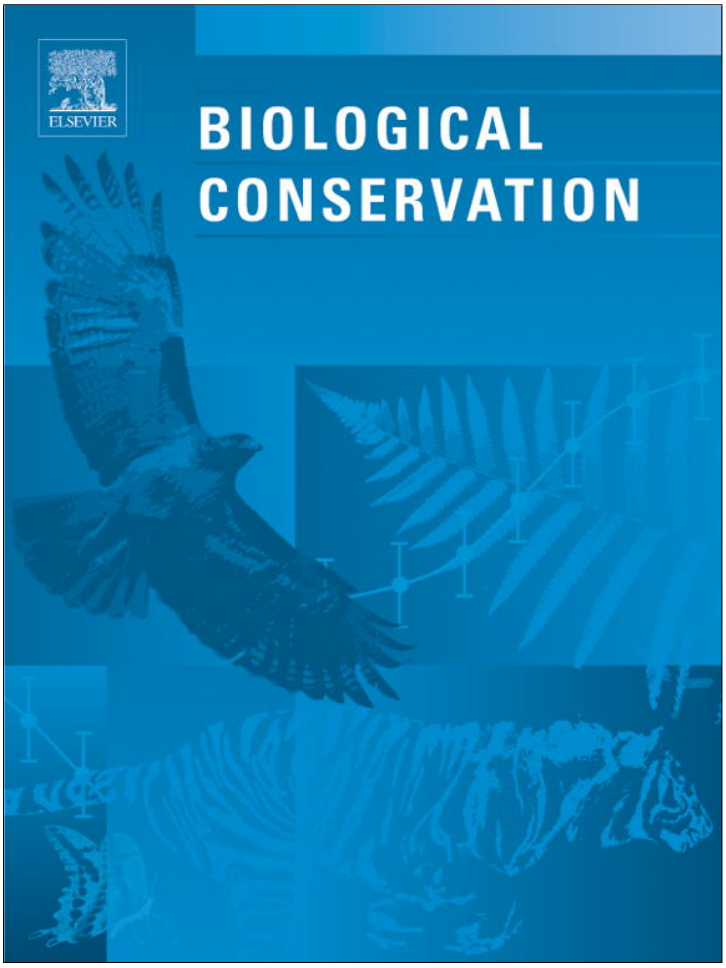
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Cryptic mammals caught on camera: Assessing the utility of range wide camera trap data for conserving the endangered Asian tapir

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A B S T R A C T

The loss and fragmentation of substantial areas of forest habitat, in combination with rampant hunting, has pushed many of Southeast Asia's megafauna species to the verge of extinction. However, the extent of these declines is rarely quantified, thereby weakening lessons learned and species-based management. This need not be the case as a proliferation of camera trap surveys for large-bodied mammals across Southeast Asia, which use a standardized sampling technique, presents a rich yet under-utilized wildlife data set. Furthermore, advances in statistical techniques for assessing species distribution provide new opportunities for conducting comparative regional analyses. Here, we focus on one of Southeast Asia's least known species of megafauna, the Endangered Asian tapir (*Tapirus indicus*), to investigate the performance of a camera trap-based spatial modeling approach in conducting a range-wide species assessment. Detection data were collectively collated from 52,904 trap days and 1,128 camera traps located across 19 study areas drawn from the Asian tapir's entire range. Considerable variation in tapir occurrence was found between study areas in: Malaysia (0.52–0.77); Sumatra, Indonesia (0.12–0.90); Thailand (0.00–0.65); and, Myanmar (0.00–0.26), with generally good levels of estimate precision. Although tapirs were widespread (recorded in 17 of the 19 study areas), their occurrence was significantly and negatively correlated with human disturbance. Thus, this study extends the previously known applicability of camera traps to include a threatened and cryptic species by identifying where and how tapirs persist (including new records of occurrence), where future surveys should be conducted and providing a benchmark for measuring future conservation management efforts.

1. Introduction

Large-bodied mammals are threatened throughout Southeast Asia. Over 10% of their forest habitat has been lost and fragmented since 2000 thereby increasing access for hunters of wildlife (Miettinen et al., 2011). In combination, deforestation and poaching have had a devastating effect on the region's megafauna (Clements et al., 2010; Corlett, 2007). For example, the Javan rhino (*Rhinoceros sondaicus*) was extirpated across most of its range from India to China to Java, due to the loss of its lowland habitats and intensive illegal hunting for its prized horn. In 2011, the species was declared extinct from Vietnam, leaving behind the last remaining population in Ujung Kulon National Park in Java (Brook et al., 2011). Likewise, Sumatran rhino (*Dicerorhinus sumatrensis*) populations have been decimated across mainland Southeast Asia, including from a former stronghold, the 13,300 km^2 UNESCO World Heritage Site of Kerinci Seblat National Park in Indonesia (Zafir et al., 2011). Furthermore, weak to non-existent law enforcement has strongly contributed to the loss of guilds of other large-bodied mammal species from several Southeast Asian countries, such as Cambodia and Vietnam (Bennett, 2011).

The ability of Southeast Asia's megafauna to recover from unrelenting hunting pressures is complicated by their generally slow reproductive rates and heightened sensitivities to human disturbances, such as forest habitat conversion (Kinnaird et al., 2003). Also, the rapid clearance and accompanying fragmentation of forest habitats across Southeast Asia, especially for oil palm cultivation (Fitzherbert et al., 2008), has had a disproportionate impact on those species with large home range requirements, such as the tiger (Wibisono et al., 2011). This situation is exacerbated as wildlife comes into closer contact and ultimately greater conflict with people. For example, the Sumatran elephant (*Elephas maximus sumatranus*) was recently placed on the IUCN Red List as Critically Endangered due to the severity of its habitat loss, hunting and retaliatory killings arising from crop-raiding (IUCN, 2012).

A fundamental requirement for protecting increasingly threatened megafauna species and populations in tropical landscapes is robust law enforcement (Leader-Williams and Milner-Gulland, 1993). Integral to this, is a clear understanding of the response of different species to this and other types of management intervention (Clements et al., 2010). Surprisingly few studies have explored the effect of physical and anthropogenic threat covariates or their proxies, such as roads, on Southeast Asia's megafauna (Rood et al., 2010; Linkie et al., 2006). As important, range-wide assessments are typically limited by a lack of comparable data sets that are confounded by different approaches to data collection and/or the shy and secretive nature of the focal species that makes it difficult to survey in the first place. However, this is changing due to the proliferation of camera trapping and recent advances in occupancy modeling techniques.

The now widespread use of camera traps for monitoring large-bodied mammals in Southeast Asia has, for the majority of recent work, been conducted according to a standardized monitoring protocol that was originally developed for estimating tiger abundance (Karanth and Nichols, 1998). Here, camera traps are placed along trails that are typically favoured by tigers, such as ridges and undistributed dirt tracks, to increase species detection probabilities. These trails are also favoured by many other large-bodied mammals that would otherwise have difficulties moving through the understory, especially in the dense humid evergreen forests of Southeast Asia. Thus, a rich yet under-utilized wildlife data set exists on many of the region's poorly studied species, which are not a primary target within the respective camera trapping projects and therefore whose data are unlikely to be analysed.

Next, through use of the robust capture-mark-recapture sampling framework, the statistical advances in distribution analyses now enable imperfect species detection to be explicitly accounted for (MacKenzie et al., 2005). In turn, this has progressed wildlife population studies beyond using a presence/absence approach, which assumes detection probability to be perfect. Thus, new opportunities exist for using camera trap data to assess the status of cryptic, threatened and/or data deficient species that were previously difficult to detect. This has been conducted for species, such as sun bears *Helarctos malayanus*, within a single landscape and holds much promise (Linkie, 2008; Wong et al., 2013). However, how this spatially explicit modeling approach performs for conducting a regional assessment remains untested, but is highly relevant for reliably assessing the conservation status of many of Southeast Asia's megafauna species.

In this study, we focus on one of Southeast Asia's least studied megafauna species, the Asian tapir, to assess the potential of camera trapping as a method that can significantly advance the science and practice of conserving cryptic and poorly studied wildlife. The Asian tapir makes an ideal case study because previous assessments have relied heavily upon expert knowledge or have pooled different types of survey data for which it was not possible to control for varying detection probabilities (Clements et al., 2012; Lynam et al., 2012; Medici et al., 2003; Shwe and Lynam, 2012) and a large body of unanalysed camera trap data potentially exists for the entire region. More specifically, we aim to conduct the first comprehensive assessment of the Asian tapir across its entire range by applying a method that explicitly accounts for imperfect species detection to model the probability of occurrence. Within this framework the influence of physical and anthropogenic threat covariates on Asian tapir probability of occurrence is then investigated. Finally, the future for this and other threatened megafauna species in each range state across the Southeast Asian region is reviewed and discussed.

2. Material and methods

2.1. Camera trap surveys

Camera traps were used to collect Asian tapir data from 19 study areas, including ten protected areas and nine unprotected areas, spanning Sumatra (Indonesia), Peninsular Malaysia, Thailand and Myanmar, the four range states in which Asian tapirs are known to occur (Table 1). Data collected at 1128 camera trap sites that were active for varying intervals of time between 1997 and 2011 were used. Of these sites, 862 (76%) were located outside of areas where Asian tapir were presumed to occur (Medici et al., 2003). Camera trap placements ranged in altitude from 1 to 1931 m asl.

The main purpose of 17 camera trap surveys was to collect data on tiger populations and their ungulate prey. Camera traps were systematically placed along ridge and animal trails to increase the probability of capturing focal species, i.e. medium to large-bodied terrestrial mammals. Whilst camera traps were not specifically set for Asian tapir, this species is most likely to use these trails (Holden et al., 2003; Linkie and Ridout, 2011), especially given its large body size (250–540 kg, Boonsong and McNeely, 1988) and the presumed higher energetic costs associated with moving off-trail through the dense understory.

Two surveys (Batang Toru and Bukit Barisan Selatan, both in Sumatra) were designed to collect data on small to large-bodied mammals, so some traps were also set off the main forest trails. However, the same approach was followed in camera trap placement in almost all of the study areas, but two, thereby minimizing heterogeneity in detectability across sites and reducing the potential associated estimator bias. Camera traps placed in all study areas were visited every 1–3 weeks to either replace film or download images, as well as to conduct maintenance checks.

2.2. Spatial database compilation

The sampling unit for this study was defined as a single camera trap placement (site) that was at least 1 km apart from the nearest neighboring camera. With this sampling unit definition, probability of occurrence represents the probability that a point in the landscape lies within a tapir home range. The location of each camera site was recorded in the field using a GPS unit and imported into ArcGIS v9.2 software (ESRI Inc., Redlands, CA). Camera traps were operational for different periods of time in the various study areas. However, for the purposes of this study we only included data from 1–90 days, with an average of 47 days per camera trap. A 24-h trapping period represented a unique sampling occasion for each of the camera trap placements. Where the original data included cameras closer than 1 km, some were discarded via random selection until this minimum separation was satisfied.

For each study site we extracted seven spatial covariates that have been shown to influence the occurrence of other large-bodied mammals in the region (Kinnaird et al., 2003), and are therefore also likely to influence Asian tapirs. These covariates comprised: elevation; slope; proximity to nearest river; proximity to nearest forest edge; protected area status; an indicator of human disturbance; and, deforestation. Elevation data, at 90 m resolution, were obtained from the Shuttle Radar Topography Mission (Rabus et al., 2003), from which the slope data layer was then derived. The river and forest edge data were obtained from various sources (Indonesian National Coordination Agency for Surveys and Mapping for Sumatra, USGS HydroSHEDS for Malaysia and for Myanmar, and IRD http://www.rsgis.ait.ac.th/~souris/thailand.htm for Thailand) and converted into individual distance coverage maps. Data on the presence of forest fires, which has been found to act as a reliable proxy for deforestation when tested for inside protected areas (Nelson and Chomitz, 2011), were obtained from the MODIS Active Fires data set (http://modis-fire.umd.edu/Active_Fire_Products.html) using the monthly temporal data that most closely matched each of the different camera trapping periods. From this, the proximity of each camera trap to the nearest fire spot was calculated. The human footprint index v.2 (Sanderson et al., 2003) was used as a proxy for general human disturbance. This 30×30 m resolution index combines a variety of indicators, such as roads, electrical infrastructure and settlements, to represent human influence on Earth. Finally, a binary covariate was created for whether a camera was located inside (1) or outside (0) a protected area boundary. Prior to analysis, the covariates were assessed for collinearity and continuous covariates were standardized using a *z*-transformation. No continuous covariates were found to be strongly correlated (Pearson's $r < 0.45$ among all pairs).

2.3. Data analysis

Asian tapir probability of occupancy (ψ) was estimated using a modeling framework that accounts for imperfect species detection (MacKenzie et al., 2005). The method explicitly models the detection process using replicate detection/non-detection data collected at sampling locations. The occupancy status of sites is assumed to remain closed (i.e. constant) during the sampling period, that is, if a point belongs to a tapir home range in the first survey day, it remains within a tapir home range on the last survey day. This is a reasonable assumption taking into account that the sampling period was at most 90 days. In its simplest form, the model describes the detection data at occupied sites as a series of independent Bernoulli trials with probability p, the probability of detecting the species during a survey replicate at an occupied site. For our analysis we considered each 24-h trapping period as an independent temporal replicate survey. The assumption of independence is reasonable, as tapirs are likely to move within their home range during this period. Unaccounted lack of independence among detections and violations of the closure assumptions can induce bias in the estimator.

According to this model, the probability of recording for instance a detection history '1011' in sampling unit i is $\psi_i p(1-p)pp$, that is, the probability that site i is occupied ψ_i and the species was detected on the first occasion (p), it was not detected on the second occasion ($1-p$), and it was detected on the third and fourth occasions (pp). The probability of observing '0000' is $(1-p)(1-p)(1-p)(1-p) + (1-\psi_i)$, that is, either the site is within the range of a tapir and the species remained undetected or the site is not used by tapirs. For the analysis, this basic model structure and an extension that accounts for abundance-induced heterogeneity in detectability were used (Royle and Nichols, 2003). The latter links species detection probability at each site p_i to individual detection probability r and local abundance (N_i) via the functional relationship $p_i = 1-(1-r)^{N_i}$, where p_i is the probability that at least one individual is detected. Since N_i is unknown, a mixture distribution is used (a Poisson with mean λ, in our analysis), and the parameters of this distribution are estimated

Table 1
Summary of range-wide field survey effort from camera trapping conducted in presumed Asian tapir habitat across Southeast Asia.

Study area	Survey dates	Landscape size (km^2)	Camera trap sampling sites			Tapir poaching within past 10 years
			Minimum convex polygon (km^2)	#	Mean elevation (m asl)	
Sumatra (Indonesia)						
Kerinci Seblat National Park[a]	September 2004–September 2009	13,300	1087	141	903	No
Batang Hari landscape[b]	November 2008–May 2009	3729	287	39	996	No
Central Sumatra[a,b]	September 2005–July 2008	28,568	2225	167	91	No
Bukit Barisan Selatan National Park[a]	September 2004–June 2006	3568	758	104	438	No
Batang Gadis National Park[a]	December 2005–July 2006	1030	122	16	998	No
Batang Toru landscape[c]	July 2008–May 2010	1350	16	14	933	Yes
Eastern Sumatra landscape[d]	March 2006–January 2008	19,384	2730	182	103	No
Malaysia (Peninsular)						
Gunung Basor Forest Reserve[e]	December 2004–February 2005	406	99	15	406	No
Temengor Forest Reserve[e]	September 2009–December 2009	1476	82	30	993	No
Taman Negara National Park[a]	December 1999–July 2001	4343	439	99	723	No
Endau-Rompin landscape[a,f]	September 2009–April 2010	3474	618	41	267	No
Thailand						
Kuiburi National Park[a]	December 2008–April 2009	969	87	25	306	No
Huai Kha Khaeng Wildlife Sanctuary[a]	December 2005–June 2006	2575	620	136	483	No
Bang Lang National Park[a]	February 1998–March 1998	261	28	19	392	No
Hala-Bala Wildlife Sanctuary[a]	May 1997–October 1997	433	29	23	277	No
Kaeng Krachan National Park[a]	January 2001–March 2001	2915	30	22	439	No
Myanmar						
Htaung Pru Forest Reserve[g]	January 2002–February 2002	310	28	18	64	Yes
Pe River Valley Forest Reserve[g]	September 2001–February 2002	285	53	20	123	Yes
Taninthayi Nature Reserve[g]	March 2011–June 2011	1700	33	17	598	Yes

[a] Strictly protected area.
[b] Conservation area set up to protect watershed forest.
[c] Predominantly production forests (assigned for plantation conversion or sustainable logging), mixed with conservation areas.
[d] Protected areas, conservation areas and oil palm plantations.
[e] Forest Reserve is primarily set up to allow sustainable logging under the Malaysian Timber Certification Scheme (limited conversion to rubber plantations is allowed in some areas).
[f] Consists of Endau Rompin Johor National Park (a protected area), Forest Reserve and Unalienated State Land (logging and conversion allowed).
[g] Non protected areas.

(λ in our case), together with the individual detection probability (r). Probability of occurrence can then be derived as the probability that at least one individual uses the site. Models were fitted using program PRESENCE 3.11 (Hines, 2006), which obtains maximum-likelihood estimates via numerical optimization.

The constant models based on the two model structures explained above, i.e. $(.)p(.)$ and $\lambda(.)r(.)$, were first fitted. Next, the effect of study area as an explanatory categorical variable was investigated by incorporating it as a covariate for occupancy (directly on ψ or through the mean abundance parameter λ) and/or for the detection parameter (p or r). Continuing the analysis with the best fitting model, we assessed the role of the seven physical and anthropogenic covariates as determinants of tapir occurrence across the region following a generalized linear modeling framework in the form of a logistic regression. Covariates were incorporated as explanatory variables for λ in a stepwise fashion, starting with one covariate, and then further adding covariates to the best fitting model, stopping when the more complicated model did not provide a better explanation for the data. Candidate models were compared using the Akaike Information Criterion (AIC).

3. Results

Asian tapir photographic records were obtained at 295 of 1,128 camera trap placements, corresponding to an overall naïve occupancy estimate of 0.26. Tapirs were detected across the whole altitudinal range of camera trap placements from sea level to 1931 m asl, including from 180 placements with detections outside of the historic known range for Asian tapir (Medici et al., 2003).

The best-fitting model accounted for abundance-induced heterogeneity in detection probability (Table 2). There was a large difference in AIC ($\Delta AIC = 83.4$) between the constant model $\lambda(.)r(.)$ and the top model, λ(study area)$r(.)$, which indicated that the probability of occurrence differed considerably among study areas (Fig. 1; Table 3). Estimates of the probability of occurrence ($\hat{\psi} \pm SE$) were highest in Batang Gadis National Park in Sumatra (0.90 ± 0.06), and in Gunung Basor Forest Reserve in Malaysia (0.76 ± 0.10). These results suggest that a high proportion of the habitat is used by tapirs in these study areas (i.e. it is likely that any given point lies within the range of at least one tapir). In contrast, occurrence probabilities were generally lowest in the

Myanmar sites. Two study areas (Pe River Valley in Myanmar and Kaeng Krachan National Park in Thailand) that lie within the presumed tapir range had no detections. The estimate of individual detection probability during a survey replicate (i.e. 24-h period) was $\hat{r} = 0.024 \pm 0.001$. Since there was no evidence of substantial differences in individual detectability across study areas, subsequent analyses were performed using a constant detection probability. The covariate analysis revealed that Asian tapir probability of occurrence was higher in habitats with lower human disturbance. The human footprint index showed a negative regression coefficient of $\hat{\beta}_{footp} = -0.022 \pm 0.007$ in the best performing model with one covariate (mC2; Table 4, Fig. 2). This model was 6.6 AIC units better than the next competing model with one covariate (mC9) and 7.8 AIC units better than the constant model (mC11). Adding further covariates did not provide a better explanation for the data. In the best model with two covariates (mC1) the estimated regression coefficient for the human footprint index remained practically the same (-0.021 ± 0.007) and the confidence interval of the coefficient for the additional covariate included zero (-0.071 ± 0.050), which suggests a non-significant effect. This was also the case for the rest of models with two covariates. While the footprint covariate captured partially the variation in occupancy across sites, the model with study area specific λ had a considerably better fit.

Table 2
Asian tapir site probability of occurrence models for the influence of the different study areas.

ID	Model	*N*	−2L	AIC	ΔAIC
mS1	λ(study area)r(.)	20	7042.0	7082.0	0.0
mS2	λ(study area)r(study area)	38	7006.6	7082.6	0.6
mS3	λ(.)r(.)	2	7161.4	7165.4	83.4
mS4	ψ(study area)p(study area)	38	7194.1	7270.1	188.1
mS5	ψ(study area)p(.)	20	7236.3	7276.3	194.3
mS6	ψ(.)p(.)	2	7362.0	7366.0	284.0

Notes: mS refers to a model from this study area analysis, ψ the probability of occupancy, λ the mean abundance parameter, p species detection probability, r individual detection probability, N number of parameters, L maximum log-likelihood, AIC Akaike Information Criterion, ΔAIC is the difference between each model's AIC and the AIC of the best model in the set.

4. Discussion

Conserving Asian tapirs, and other megafauna species, across the Southeast Asian region is predicted to become even more challenging in the next decade. Presently, the economies of most Southeast Asian countries are booming. There is a high demand for natural resources, while human populations are rapidly expanding and growing in an already densely populated region (OECD, 2011). From our study, the importance of human disturbance as a negative factor in explaining tapir occurrence is a sobering reminder of this challenge. By collating one of the largest data sets of camera placements available for a single species, this study has provided previously lacking information on the distribution of one of Southeast Asia's least studied species. The Asian tapir occupancy information collected in each of its range states also provides valuable insights into the management interventions required to conserve remaining populations within the respective countries.

4.1. Sampling protocol

Large-bodied mammals living in tropical evergreen forests are notoriously difficult to survey. Nevertheless, the modeling technique used in this study allowed us to account for imperfect detection and to apply this to analysing a large data set that led to relatively precise estimates of Asian tapir occurrence and detection probabilities. Similar data and analyses could be used to systematically assess the status of Southeast Asia's many other megafauna species, such as elephant or gaur (*Bos gaurus*). Indeed, most of the study areas from which data were derived for this study already have rich photographic data sets of other mammal species, including sun bear (*Helarctos malayanus*) and clouded leopard (*Neofelis sp*; Wong and Linkie, 2012). Whilst important to respective IUCN/SSC Specialist Groups, such single-species datasets are unlikely to be centrally compiled and/or systematically analysed. Thus, wide-scale collaborations such as this one for tapirs, and as conducted for tigers (Wibisono et al., 2011; Dinerstein et al., 2007), should be encouraged. For Asian tapirs, repeating the camera trap surveys in the same study areas would enable a scientific assessment of the species's population trend, as has been recently achieved through monitoring changes in sun bear occupancy (Wong et al., 2013).

Four aspects of our sampling approach need to be considered further in the interpretation of the results. First, given the definition of sampling sites as camera trap placements, the probability of occurrence reflects the proportion of habitat that lies within at least one individual home range and therefore is a joint function of density and home range size (Efford and Dawson, 2012). While occupancy can be a useful state variable, it is important to realize that if large variations in home range size are expected across study areas, which is not considered to be the case for Asian tapirs, no direct conclusions about differences in density can be made using occupancy statistics. Similarly, occupancy estimates might not reflect well temporal density trends if the home ranges of a species significantly expand or contract as a function of density.

Second, this data set comprised various independent surveys targeted at small sections within particular study areas. Although the data set has a good overall spatial coverage, the sampling was not random and so the overall estimate is not necessarily representative of the entire tapir range, especially as our surveys tended to focus on protected and conservation areas. To avoid overstating the results in regional occupancy-based studies such as ours, it is therefore important to present information on the size of the areas in which camera traps are set within their respective landscapes (i.e. Table 1).

Third, data from several study areas were collected pre-2000. Therefore, while the results of this study represent the best available knowledge on the distribution of Asian tapirs, the situation in these areas might have changed, especially as two study areas in southern Thailand now fall within an area subject to an insurgency movement. Where possible, we recommend that repeat surveys should be conducted to update these areas. Furthermore, we recommend that new surveys be conducted in human-altered landscapes, such as those containing mosaics of secondary forest, oil palm plantations and rubber plantations (Fig. 1). Such landscapes may contain tapirs but they were under-represented in this study.

Fourth, the human footprint index was developed more than 10 years ago (Sanderson et al., 2003) and will have changed since then. For study areas with more recent data, this suggests that the current disturbance effect is likely to be more pronounced than that previously captured in the human footprint index and that, in turn, Asian tapirs may actually be more resilient to disturbance than currently portrayed.

4.2. Asian tapir conservation and ecology

The Asian tapir is an important disperser of small-seeded plants (Campos-Arceiz et al., 2012). It is therefore likely to play a more limited ecological role compared with Southeast Asia's other

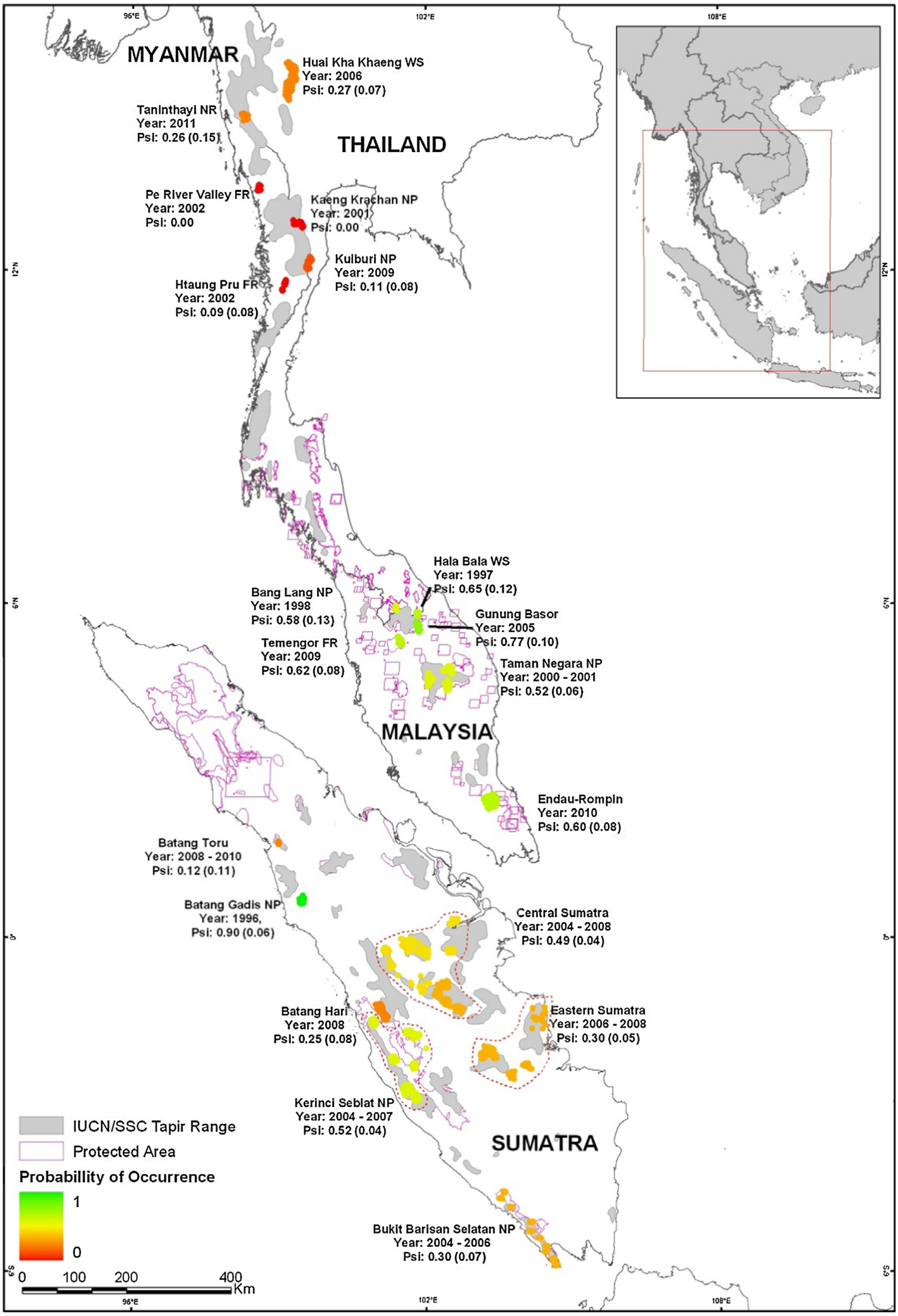

Fig. 1. Probability of Asian tapir occurrence (Psi) from 1128 camera trap placements set in 19 study areas across Southeast Asia.

megafauna species, such as elephants and rhinos that routinely disperse large seeds in addition to those of small-seeded plants (Campos-Arceiz et al., 2012). Therefore, although the long-term impact of the extirpation of tapirs from functioning forests in Southeast Asia is not known, it is likely to be less acute than that of elephants (Campos-Arceiz and Blake, 2011).

Hunting of Asian tapir is not considered to be a primary threat across its range states (Corlett, 2007). In contrast, encroachment at

Table 3
Asian tapir site probability of occurrence ($\hat{\psi}$) estimates for each study area obtained from the best model.

Study area	S	K_t	K	S_d	d	$\psi_{naïve}$	$\hat{\psi}$ (±SE)
Sumatra (Indonesia)							
Kerinci Seblat National Park	141	11,533	82	66	182	0.47	0.52 (0.04)
Batang Hari Protection Forest	39	2929	75	8	15	0.21	0.25 (0.08)
Central Sumatra	167	11,172	67	58	180	0.35	0.49 (0.04)
Bukit Barisan Selatan National Park	104	2408	23	14	19	0.13	0.30 (0.07)
Batang Gadis National Park	16	425	27	12	19	0.75	0.90 (0.06)
Batang Toru landscape	14	531	38	1	1	0.07	0.12 (0.11)
Eastern Sumatra landscape	182	4183	23	23	39	0.13	0.30 (0.05)
Malaysia (Peninsular)							
Gunung Basor Forest Reserve	15	819	55	10	23	0.67	0.77 (0.10)
Temengor Forest Reserve	30	2551	85	19	46	0.63	0.62 (0.08)
Taman Negara National Park	99	5637	57	31	117	0.31	0.52 (0.06)
Endau-Rompin landscape	41	2664	65	19	60	0.46	0.60 (0.08)
Thailand							
Kuiburi National Park	25	1406	56	2	3	0.08	0.11 (0.08)
Huai Kha Khaeng Wildlife Sanctuary	136	2181	16	12	18	0.09	0.27 (0.07)
Bang Lang National Park	19	606	32	8	10	0.42	0.58 (0.13)
Hala-Bala Wildlife Sanctuary	23	573	25	9	13	0.39	0.65 (0.12)
Kaeng Krachan National Park	22	805	37	0	0	0.00	0.00 (–)
Myanmar							
Htaung Pru Forest Reserve	18	728	40	1	1	0.06	0.09 (0.08)
Pe River Valley Forest Reserve	20	1207	60	0	0	0.00	0.00 (–)
Taninthayi Nature Reserve	17	546	32	2	5	0.12	0.26 (0.15)
Overall	1128	52,904	47	295	751	0.26	0.43 (0.02)

Notes: S number of sampling sites (i.e. traps >1 km a part), K_t total number of trap days in the study area, K average number of trap days per trap, S_d number of traps in which tapirs were detected at least once, d total number of detections, $\psi_{naïve}$ occupancy estimate (i.e. S_d/S), $\hat{\psi}$ occupancy estimate based on model mS1 (Table 2).

Table 4
Asian tapir site probability of occurrence models for the influence of the different site specific physical and anthropogenic threat covariates.

ID	Model	N	−2L	AIC	ΔAIC
mC1	λ(footp + elev)r(.)	4	7149.6	7157.6	0.0
mC2	λ(footp)r(.)	3	7151.6	7157.6	0.0
mC3	λ(footp + dRiv)r(.)	4	7149.6	7157.6	0.0
mC4	λ(footp + PA)r(.)	4	7150.1	7158.1	0.5
mC5	λ(footp + slope)r(.)	4	7151.3	7159.3	1.7
mC6	λ(footp + fire)r(.)	4	7151.4	7159.4	1.9
mC7	λ(footp + dEdge)r(.)	4	7151.5	7159.5	1.9
mC8	λ(all)r(.)	9	7143.5	7161.5	3.9
mC9	λ(dRiv)r(.)	3	7158.2	7164.2	6.6
mC10	λ(elev)r(.)	3	7158.5	7164.5	7.0
mC11	λ(.)r(.)	2	7161.4	7165.4	7.8
mC12	λ(dEdge)r(.)	3	7160.1	7166.1	8.6
mC13	λ(PA)r(.)	3	7160.8	7166.8	9.3
mC14	λ(slope)r(.)	3	7161.0	7167.0	9.4
mC15	λ(fire)r(.)	3	7161.4	7167.4	9.8

Notes: mC refers to a model from this physical and anthropogenic covariate analysis, λ the mean abundance parameter, r individual detection probability, N number of parameters, L maximum log-likelihood, AIC Akaike Information Criterion, ΔAIC is the difference between each model's AIC and the AIC of the best model in the set; model covariates are abbreviated as 'footp' (human footprint index), 'elev' (elevation), 'PA' (protected area status), 'fire' (a deforestation proxy), 'dRiv' (distance to nearest river) and 'dEdge' (distance to nearest forest edge).

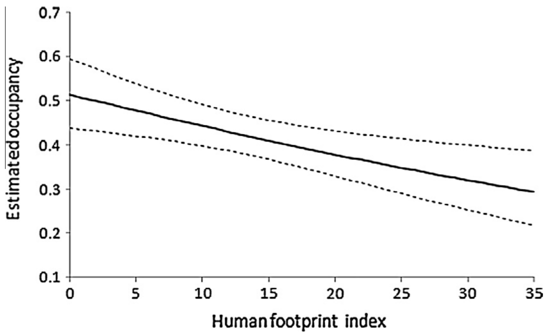

Fig. 2. Estimated relationship of predicted Asian tapir occupancy as a function of the human footprint index (±SE).

forest edges and park boundaries is a serious threat in many parts of the forest dependent tapir's range. This effect may have been captured in the human footprint index, which includes infrastructure, such as roads, which are often important drivers of tropical deforestation (Linkie et al., 2004). Therefore, a conservation strategy that protects the forest border of conservation areas is strongly recommended, as is spatial planning that adequately considers environmental impacts from infrastructure development. Other relationships between tapir occurrence, threats and strategies to mitigate these, may vary between range states, and are discussed below.

4.3. Sumatra

Asian tapirs are rarely hunted in Sumatra because the predominantly (>90%) Muslim population does not eat its meat. This custom is at least partly explained because the tapir is often mistakenly considered a close relative of the wild boar, whose meat consumption is prohibited under Islam (Holden et al., 2003). However, in Batang Toru, where there the majority (67%) of people are not Muslim, tapirs are hunted at a low level (approximately 1% of the 2900 people interviewed; Fredriksson unpublished data) Despite the biogeographical riddle as to why Asian tapirs have never occurred in the northern most part of Sumatra, such as Aceh province, the relatively high probability of occurrence of tapirs across other areas of Sumatra is probably explained by the combination of large protected areas that still contain sizeable tracts of primary rainforest. Furthermore, the extensive areas of degraded primary forest in Central Sumatra (Riau province) and Eastern Sumatra (Jambi province), which are undergoing the most rapid conversion in Southeast Asia, were still found to contain tapirs ($\hat{\psi} = 0.49$ and 0.30, respectively). Nevertheless, the high and unrelenting rates of island-wide forest clearance for agriculture, and the associated human disturbance, are of conservation concern, having on average exceeded 2%/yr for the past two decades (Uryu et al., 2010).

The impact of converting forest habitats on Sumatra's wildlife, particularly on large-bodied mammals, has been most intensely felt outside of protected areas (Uryu et al., 2010). However, the protected areas themselves, which should act as strongholds for the Asian tapir and other megafauna species, have now come under direct threat themselves. For example, Kerinci Seblat National Park has been placed on the In Danger list of World Heritage Sites by UNESCO because of ongoing illegal land clearance and a proposal to construct three large asphalt roads that would severely fragment key tapir forest habitat within the national park. In many ways the fate of Asian tapirs, and indeed other large-bodied mammals, is epitomised by the situation found in Batang Gadis National Park in North Sumatra. This area had a high probability of occurrence for tapirs (0.90), but instead of offering hope for the species's survival, some 30% of the 1,030 km^2 national park has recently been excised for open-cast gold mining (GoI, 2004).

4.4. Malaysia

In Malaysia, the relatively high probabilities of occurrence recorded for Asian tapirs could be partly attributed to the low hunting pressure directly affecting this species (Kawanishi et al., 2002). Furthermore, forests appear to be better managed in Peninsular Malaysia than, for example, in Sumatra (Miettinen et al., 2011). Indeed, the highest Asian tapir estimates for the country were reported from forest reserves where public access is restricted and selective logging is expected to follow reduced impact logging protocols. In fact, species distribution models have shown that selectively logged forests in Peninsular Malaysia encompass more than half of the areas identified as suitable tapir habitat (Clements et al., 2012). A likely biological explanation for the high probability of tapir occurrence in selectively logged forests is the more open forest canopy, which allows more direct sunlight into the understory, and therefore increases browse availability for ungulates (Davies et al., 2001) such as the tapir. As a result, carnivores such as tigers, which can be sensitive to human disturbances, also still persist in Malaysia's selectively logged forests. Indeed, the highest population density estimate for tigers has so far been reported from Gunong Basor Forest Reserve (Rayan and Shariff, 2009), the area which our analysis estimated as having the highest probability of tapir occurrence.

To ensure that tapir conservation remains a high priority in Malaysia, existing species action plans, such as the National Tiger Conservation Action Plan for Malaysia (DWNP, 2008), which offers benefits to concurrent species, should continue to be implemented and monitored. Pertinent actions would relate to improving management of selectively logged forests (Giam et al., 2011; Rayan et al., 2012), securing large continuous forests linked with ecological corridors and ensuring that law enforcement patrols protect forest habitat and remove snare traps (Clements et al., 2012). Although such traps are not set specifically for Asian tapir, they indiscriminately capture and kill this and other threatened species of wildlife (Gumal et al., 2012). Most importantly, legal clear-felling within forest reserves for the planting of monoculture tree crops such as timber-latex clones should be prohibited (Aziz et al., 2010).

4.5. Thailand

The current situation for Asian tapirs in Thailand is more promising than in the past since large-scale forest loss, and its associated high disturbance, has been arrested following a national ban on commercial logging in 1989. Presently, limited forest encroachment around the edges of forest reserves and protected areas, pose the key threats to the species (Lynam et al., 2012). Tapirs used to be hunted around the Kuiburi study area more than 20 years ago, but there is no evidence this practice continues or that it ever was a principal threat (Steinmetz, pers. comm.). Thus, there is no recent evidence of directed tapir poaching in Thailand, although tapirs potentially fall into snares set for other large mammals, as can also occur in the other range states (Holden et al., 2003). While tapirs in Kaeng Krachan National Park were not detected by camera-traps in 2001–2002, analysed data corresponded to surveys that focussed on the section most heavily visited by tourists. Consequently, this site might not be representative of the wider area and/or it had an insufficient sampling effort, as a subsequent survey (2003–2004) in a lower elevation area recorded two tapir detections from 4805 camera trap nights across a 34 km^2 sampling area (Lynam et al., 2012).

4.6. Myanmar

A combination of factors likely explains the absence or low occurrence of Asian tapirs in the Myanmar study areas. The first is a possible sampling limitation because there were only three study areas in this country and each covered a small area (28–53 km^2), which may not have adequately represented the wider landscape. Secondly, tapirs in Myanmar face a wide range of direct threats, including poaching for their meat and as trophies, accidental snaring and forest habitat conversion for agricultural plantations, all of which is exacerbated by weak conservation management (Shwe and Lynam, 2012). Only 7.7% of the 22,000 km^2 of forest habitat available for tapirs in the Taninthayi region is covered by a single protected area, the Taninthayi Nature Reserve. Recovering tapirs in Myanmar will first require additional forest areas in the south to be brought under formal protection and a more intensive effort to protect the current forest habitat by reducing poaching and eliminating illegal wildlife trade. Thus, strengthening protected area management is critical. Unlike in other range states, a country conservation plan for large mammals, including Asian tapirs, is urgently required for longer-term species management. Finally, the key recommendations from the National Tiger Action Plan (Lynam, 2003) that includes reducing the killing and associated trade of tiger prey species, maintaining connectivity of habitat across country borders, and creating new protected areas in southern Myanmar, should all benefit Asian tapirs.

5. Conclusion

Across the tropics, rampant deforestation and increasing hunting pressures have locally extirpated many large-bodied mammal populations (Corlett, 2007; Harrison, 2011). Yet, despite the widespread threats facing Southeast Asia's megafauna, one of the region's largest animals, the Asian tapir, was found to be widespread, with 90% of the study areas containing tapirs. Even more encouragingly, Asian tapirs still had high a probability of occurrence (i.e. around 0.50 or greater) in nine of the study areas. Nevertheless, several locations that were widely surveyed (>80 km^2) had low occurrence, which may bear witness to the vulnerability of Asian tapirs to anthropogenic impacts both inside and outside of protected areas. This study extends the previously known applicability of camera traps to include a threatened and cryptic species by identifying where and how tapirs persist (including new records of occurrence), where more representative surveys are needed, as well as providing important insights into ensuring the survival of one of Southeast Asia's least known species of megafauna. It also provides a benchmark and sampling protocol for measuring future conservation management efforts, which has wide applicability to threatened, cryptic and/or poorly studied large-bodied mammal species.

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