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Quantifying changes in sun bear distribution and their forest habitat in Sumatra

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Abstract

High rates of deforestation are presumed to adversely affect large-bodied mammal populations across South-east Asia. Understanding how these species respond to deforestation is therefore important for their conservation, particularly for more cryptic species that have proved a challenge to enumerate. Here, we use an occupancy approach based on detection/non-detection data collected over two survey periods to conduct the first assessment of spatio-temporal changes in sun bear distribution. We measured sun bear population trends through repeat camera-trap surveys and assessed their response to varying levels of deforestation in four study areas located in and around the 13 300 km^2 Kerinci Seblat National Park (KSNP), Sumatra, from 2004/06 to 2009/11. The crude results suggested a decline in sun bear distribution, from 0.683 [0.519–0.810; 95% confidence intervals (CIs)] to 0.444 (0.253–0.584), but there were considerable overlaps in temporal CIs. This overall change in occupancy was partially driven by the significant decline (9.4%$year^{-1}$) in one subpopulation living in the study area that underwent the highest rate of deforestation (0.96%$year^{-1}$). Meanwhile, sun bear subpopulations living in areas experiencing lower deforestation rates (i.e. < 0.60%$year^{-1}$) appear to be less affected by forest clearance. Our study demonstrates that occupancy modelling is a useful and replicable tool for monitoring sun bear populations in KSNP and elsewhere. Our results confirm that KSNP is a stronghold for sun bears, while also forewarning of the detrimental effects of ongoing illegal deforestation on sun bear distributions.

Introduction

Large-bodied mammals across South-east Asia face the twin threats of poaching, whether for their meat or for trade in their body parts, and of habitat loss arising from rapid deforestation (IUCN, 2011). The tropical rainforests of Sumatra, Indonesia, represent important habitats for many critically endangered large-bodied mammals, such as elephant, tiger and orangutan (Hedges *et al*., 2005; Linkie *et al*., 2006; Campbell-Smith *et al*., 2011). However, high rates of forest conversion to agricultural lands such as oil palm plantations represent a significant threat to the survival of such species (Fitzherbert *et al*., 2008). From 2000–2008/09, Sumatran rainforests were converted at an island-wide rate of 2.3%$year^{-1}$, while Riau province alone lost 1.6 million ha of rainforest, representing 48% of its entire forest estate during the same period (Uryu *et al*., 2010).

Understanding how large-bodied mammals respond to changing ecological conditions, such as forest conversion, and to the impact of illegal activities that might both threaten their future survival is crucial. In order to develop cost-effective conservation management strategies and to measure their impact, research on threatened species should initially focus on developing baseline information such as estimating their density, occupancy and abundance (Kawanishi & Sunquist, 2004; Soisalo & Cavalcanti, 2006), and determining relationships with threat proxies such as distance to forest edge or roads (Kinnaird *et al*., 2003). Although this baseline information and associated analyses are important, it is vital over the longer term to repeat standardized surveys that are sufficiently precise to identify population trends that, in turn, enable quantitative evaluations of the impact of conservation actions (Danielsen *et al*., 2009).

The introduction of camera-trap surveys has greatly increased the amount of information on secretive and cryptic species in tropical rainforest habitats (Rowcliffe & Carbone, 2008). The capture of these data within robust sampling frameworks that explicitly account for unequal detection probabilities has mainly enabled range-wide comparisons of, for example, the population densities of jaguars (Silver *et al*., 2004) and tigers (Karanth & Nichols, 1998) and a few studies on their population trends (Karanth *et al*., 2006; Wegge *et al*., 2009). Nevertheless, it is often difficult to

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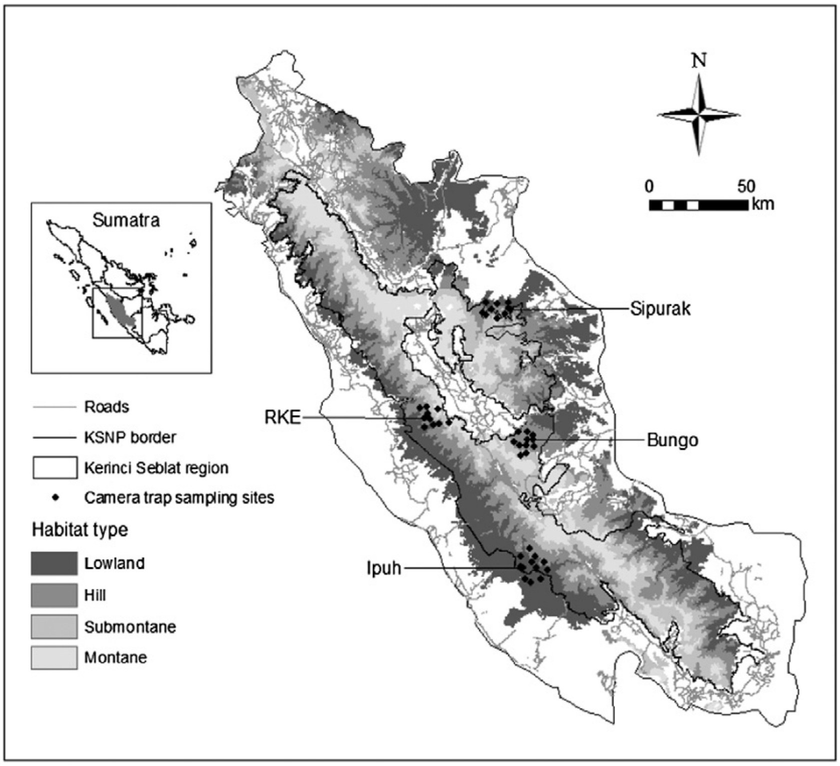

Figure 1 Sun bear *Helarctos malayanus* camera-trap monitoring sites in and around the 13 300 km^2 Kerinci Seblat National Park (KSNP), Sumatra. RKE, Renah Kayu Embun.

identify individuals of many tropical mammal species, thereby precluding estimates of density and their trends, which is especially important for threatened species.

The sun bear *Helarctos malayanus* is a case in point. Despite being upgraded from Data Deficient to Vulnerable in 2007 (IUCN, 2011), field data on sun bears are scarce, thereby hampering the development of conservation plans. Consequently, the International Union for Conservation of Nature/Species Survival Commission (IUCN/SSC) Bear Specialist Group has prioritized the development of a standardized system to monitor sun bear population trends. The IUCN/SSC Sun Bear Expert Team currently estimates global sun bear populations have decreased by 30% over the past 30 years (three generations; IUCN, 2011). This estimate is based on the decline of suitable sun bear habitats, which serves as a proxy for species population status (Servheen, 1999).

Sun bears are difficult to study in the wild due to their shy and cryptic behaviour. However, through adaptation of Pollock's (1982) robust capture–mark–recapture framework, Linkie *et al.* (2007) were able to provide the first estimates of sun bear occupancy through a detection/non-detection sampling technique using camera-trap data, which this study seeks to enhance and repeat. Occupancy estimates derived from detection/non-detection survey data provide an effective approach for assessing the spatio-temporal patterns in species distribution when a species is not always detected with certainty (Nichols *et al.*, 2008). Although this approach has been applied to a wide range of taxa such as amphibians, avifauna and mammals (O'Brien & Kinnaird, 2008; Sewell, Beebee & Griffths, 2010; Karanth *et al.*, 2011), its use in monitoring programmes at a landscape level, particularly for threatened large-bodied mammals that are difficult to study, is lacking. Here, we aim to evaluate changes in a sun bear population, using occupancy as the state variable, across the Kerinci Seblat (KS) region of Sumatra, in response to the threat posed by varying levels of deforestation.

Methods

Study area

The KS National Park (NP), located in west-central Sumatra (Fig. 1) is one of the largest protected areas in Asia and is considered to be a stronghold for many large-bodied mammal flagship species including Sumatran tiger and Asian tapir (Holden, Yanuar & Martyr, 2003; Linkie *et al.*, 2006), as well as of sun bears (Tumbelaka & Fredriksson, 2006). However, these species face varying degrees of threat from poaching and/or deforestation, which have also led to the recent extirpation of Sumatran rhino and two of the KSNP's three elephant subpopulations (Zafir *et al.*, 2011). Illegal hunting of ungulates and tigers occurs in KSNP, but not to the extent found across mainland South-east Asia. In KSNP, poaching impacts may be minimal, as indicated by the widespread occurrence of tigers (Wibisono *et al.*, 2011), resulting from raised levels of effective law enforcement patrols (Hartana & Martyr, 2010). Sun bears are not targeted by poachers in KSNP, and from extensive law enforcement patrols, only one report exists of a sun bear being caught in a snare trap that had been set for wild boar

Table 1 Camera-trap study areas used for estimating sun bear *Helarctos malayanus* occupancy in and around Kerinci Seblat National Park (KSNP), Sumatra

Study area	Camera-trap area (km^2)	Altitudinal range (and mean) in m	Habitat type	Protection status	Camera-trapping period	
Sipurak	88	694–1254 (901)	Primary hill	Inside KSNP	Jan–Mar 2005[a]	Dec 2009–Mar 2010
Bungo	90	363–1745 (753)	Degraded lowland/ hill forest	Predominantly inside ex-logging concession with a few sites inside KSNP	Apr–July 2006[a]	Apr–July 2010
RKE	104	947–1941 (1194)	Primary submontane	Inside KSNP	Sept–Nov 2004[a]	Aug–Nov 2010
Ipuh	118	194–1064 (511)	Degraded lowland forest	Predominantly inside ex-logging concession with a few sites inside KSNP	Aug–Dec 2006[b]	Nov 2010–Feb 2011

[a]Data taken from Linkie *et al.* (2007).
[b]Data taken from Linkie *et al.* (2008*a*).
RKE, Renah Kayu Embun.

(Hartana & Martyr, 2001). Hitherto, no reports exist of trade in sun bear gall bladder from KSNP, where deforestation remains the most prominent threat faced by the species.

Consequently, this study focused on determining the influence of deforestation on changes in sun bear distribution in two areas inside KSNP and two areas that straddle the KSNP border and extend into the wider KS region. In combination, camera traps covered all of the main tropical forest types in which sun bears are known to live. These range from selectively logged and primary lowland-hill forest to pristine montane forests that varied in levels of forest degradation and protection status (Table 1).

Sampling design and data

Camera traps were set in four study areas previously used by Linkie *et al.* (2007, 2008*a*). Data from these previous studies were used to develop a baseline occupancy estimate from 2004–2006 that was compared with repeat survey data collected from 2009–2011 (Table 1).

A combination of Photoscout (PTC Technologies Inc, Boston, MA, USA), Moultrie (Moultrie™, Alabaster, AL, USA) and Bushnell (Bushnell Corporation, Overland Park, KS, USA) infrared camera traps, activated by motion sensors, was placed along ridge and animal trails at a height of approximately 0.5 m above the ground. Cameras were active 24 h day^{-1}, set with a 1-min delay between exposures. The cameras were programmed to record the time and date of each event and were active for approximately 3 months at each sampling site for both survey periods to minimize the likelihood of violating an assumption that the population was demographically closed over K sampling occasions (Otis *et al.*, 1978). Cameras were visited every 2 weeks to replace their film, memory cards, batteries and to check their condition. A study area was defined as lying within the outermost camera locations joined to form a unique boundary.

To measure sun bear occupancy, a sampling unit was assumed to be closed, that is, an individual sun bear, if present within a unit, had a nominal detection probability over all sampling occasions. Thus, the sampling unit size used was based on that of an individual sun bear's home-range size, that is, 14.8 km^2 (Wong, Servheen & Ambu, 2004). Subsequently, we extend the work conducted by Linkie *et al.* (2007), which previously set trap spacing at 1.5–4 km, by increasing the minimum trap spacing to 4 km apart for datasets from both sampling periods. Where two cameras were in closer proximity, one was randomly removed.

Data compilation

Sun bear occupancy in the KS region is likely to be influenced by biophysical and anthropogenic factors. Therefore, a spatial dataset of seven potential variables was constructed within ArcGIS v9.3 software (ESRI, Redlands, CA, USA). An additional two categorical variables, study area and forest type, were included in the modelling process. Variable data were obtained from several sources: elevation and slope (Rabus *et al.*, 2003) extracted at a 30-×-30-m resolution within each sampling site; distance to roads, logging roads, rivers and villages (Indonesian National Coordination Agency for Surveys and Mapping); and distance to forest edge (from within the forest). Forest type was categorized as either primary forest (1) or logged (0). The principal reason for including these variables was to control for the possible influence of confounding variables and therefore enable more reliable assessments of change in occupancy.

The continuous data extracted from each sampling site from both survey periods were imported into SPSS v.18.0 (SPSS, Chicago, IL, USA) and logarithmically transformed to reduce the disproportionate influence of outliers. To test for non-independence between variables, a Spearman's Rank Correlation Coefficient (r_s) was performed. Thus, the covariates' distance to roads and villages ($r_s = 0.78$), distance to forest edge and villages ($r_s = 0.62$), and distance to logging roads and elevation ($r_s = 0.55$) were correlated ($P < 0.01$) and subsequently combined using a data reduction technique (Principle Component Analysis) to produce a single covariate for the final dataset. Consequently, the resultant variables were road/village, forest edge/village and logging/elevation. Due to the possibility of non-independence between camera-trap sampling sites, the

Spatial Statistics Toolset extension in ArcGIS v9.3 was used to test for the presence of spatial autocorrelation across sampling unit coordinates by calculating Moran's *I* statistic.

GIS forest cover maps derived from Landsat satellite imagery were obtained for the years 2004 and 2008/09 for the KS region. Data from 2004 were provided by Linkie *et al.* (2007) and from 2008/09 by World Wildlife Fund (WWF)-Indonesia (Uryu *et al.*, 2010). Deforestation was defined as the complete conversion of forest to non-forest over this period. The forest cover maps were used to calculate the area of forest loss and the mean deforestation rate from 2004–2008/09 across the KS region. Deforestation rates were measured at each study area by creating an appropriate buffer of 4 km based on sun bear home-range size (Wong *et al.*, 2004) around the camera-trapping polygon of the outermost cameras forming an effective sampling area.

Estimating sun bear occupancy

This study followed a robust sampling design (Pollock, 1982; Mackenzie *et al.*, 2002) where a number of sample sites (n) were visited multiple times on K sampling occasions. For each of the two survey periods, sun bear occupancy was estimated using a likelihood-based method (MacKenzie *et al.*, 2002). From field surveys, the detection (1) or non-detection (0) sequence of sun bears over six consecutive 2-week sampling occasions per study area was recorded and used to construct a detection history. Detection histories were produced for each of the four study areas and entered together as one dataset into PRESENCE v2.3 software (Hines, 2006) representing a global KSNP model. Single-species, single-season analyses were run for the datasets collected from 2004/06 and 2009/11 to compare occupancy estimates between the two periods.

Occupancy and detection probability were modelled first as if constant across sites and samples, $\psi(.)p(.)$, and second as functions of the variables (MacKenzie *et al.*, 2006). Detection probability was modelled as a function of forest type to account for the difference in large tree density across habitat types. The variables were incorporated within the occupancy model whereby a logistic regression type analysis was performed to determine the variables that best explained overall sun bear occupancy ($\hat{\psi}$) for KSNP. The variables in the modelling process were incorporated, either individually or in combination, restricting models to a maximum of two variables in any one model (Sewell *et al.*, 2010), with the aim of producing the smallest 95% confidence intervals (CIs). Candidate models were ranked based on their delta second-order information criterion (ΔAIC_c) values and their Akaike weights (w_i; Burnham & Anderson, 2002).

Because study area was modelled as a function of occupancy (ψ(study area)$p(.)$), the corresponding beta coefficients derived from PRESENCE were used to estimate sun bear occupancy for each study area using the following equation:

$$P = \frac{1}{1 + e^{-(\beta_o + \sum \beta_i X_i)}},$$

where β_o is the constant coefficient (intercept) and $\beta_1, \beta_2 \ldots \beta_i$ represent the regression coefficients of the associated independent variables $X_1, X_2 \ldots X_i$.

The 95% CIs derived from the PRESENCE software were used to test for significant changes in occupancy between survey periods, both for the global KSNP model and for individual study areas. Non-overlapping 95% CIs indicated a significant difference in occupancy. However, CIs that overlap slightly may also imply a significant change. Consequently, a Wald test was performed to provide an independent and robust measure of change, with the $P < 0.05$ considered to be significant (i.e. $Z > 1.96$).

Results

Deforestation rates

From 2004–2008/09, a total of 932.2 km^2 of forest was cleared across the KS region, at a mean deforestation rate of 1.10%year^{-1}. The mean annual deforestation rate (%year^{-1}) varied across the four individual study areas, from high (0.96) in Bungo, to medium (0.52) in Sipurak and to low (0.11–0.13) in Ipuh and Renah Kayu Embun (RKE), respectively.

Single-season occupancy

From the 2004/06 survey, 39 independent camera placements produced a sampling effort of 3817 trap nights. Sun bears were detected in 23 of the units, corresponding to a naive occupancy estimate of 0.615. The constant model $\psi(.)p(.)$ estimated sun bear occupancy ($\hat{\psi} \pm \text{SE}$) to be 0.730 ± 0.09, whereas the top-ranked model produced an occupancy estimate of 0.683 ± 0.07 (Table 2; Model 1.1).

From the 2009/11 surveys, 40 camera placements over 3786 trap nights detected sun bears in 17 placements, corresponding to a naive occupancy estimate of 0.425. The constant model estimated sun bear occupancy to be 0.445 ± 0.07 (Table 2; Model 2.3), and the top-ranked model produced an occupancy estimate of 0.444 ± 0.09 (Table 2; Model 2.1).

Modelling study area as a function of occupancy from the first period produced the following beta coefficient values [$\beta_i \pm$ standard error (SE)]; $\beta_{Sipurak} = -0.262$ (0.974), $\beta_{Bungo} = 2.335$ (1.237), $\beta_{RKE} = -0.571$ (1.011) and $\beta_{Ipuh} = 0.050$ (0.686) and respective occupancy estimates ($\hat{\psi} \pm \text{SE}$), 0.447 (0.109), 0.916 (0.111), 0.373 (0.106), 0.512 (0.102). From the second period, the following beta coefficient values ($\beta_i \pm$ SE); $\beta_{Sipurak} = 0.979$ (0.962), $\beta_{Bungo} = 0.901$ (0.940), $\beta_{RKE} = -0.195$ (0.941) and $\beta_{Ipuh} = -0.608$ (0.631), produced the occupancy estimates ($\hat{\psi} \pm \text{SE}$) of 0.592 (0.101), 0.573 (0.110), 0.309 (0.105) and 0.353 (0.104), respectively.

Spatio-temporal population trends

Across the KS region, the global sun bear occupancy showed an overall decrease of 35.0%, at a rate of 5.0%year^{-1} over 7 years. However, this trend was not significant because

Table 2 Estimated sun bear *Helarctos malayanus* occupancy ($\hat{\psi}$) and detection probability ($\hat{p}$) from the top-ranked models for Kerinci Seblat National Park and surrounding forest for survey periods, 2004/06 and 2009/11

Model no.	Models	ΔAIC_c	w_i	K	$\hat{\psi}$ (± SE)	95% CIs	$\hat{p}$
First period (2004/06)							
1.1	ψ(road)p(.)	0.00	0.246	3	0.683 (0.075)	(0.519–0.810)	0.285
1.2	ψ(village/road)p(.)	0.08	0.236	3	0.699 (0.098)	(0.435–0.877)	0.278
1.3	ψ(road + forest edge)p(.)	1.62	0.109	4	0.719 (0.071)	(0.526–0.855)	0.270
1.4	ψ(village/road + elev)p(.)	1.79	0.100	4	0.720 (0.104)	(0.485–0.906)	0.270
1.5	ψ(village/road)p(forest type)	2.22	0.081	4	0.701 (0.097)	(0.449–0.876)	0.275
1.6	ψ(road)p(forest type)	2.30	0.078	4	0.684 (0.075)	(0.519–0.812)	0.283
1.7	ψ(road + elev)p(.)	2.36	0.076	4	0.748 (0.054)	(0.538–0.865)	0.259
1.8	ψ(road + forest type)p(.)	2.38	0.075	4	0.684 (0.099)	(0.435–0.827)	0.285
Second period (2009/11)							
2.1	ψ(elev)p(.)	0.00	0.154	3	0.444 (0.107)	(0.253–0.584)	0.443
2.2	ψ(village)p(.)	0.24	0.136	3	0.444 (0.090)	(0.269–0.608)	0.444
2.3	ψ(.)p(.)	0.35	0.129	2	0.445 (0.082)	(0.254–0.596)	0.443
2.4	ψ(village/road)p(.)	0.65	0.111	3	0.444 (0.106)	(0.250–0.613)	0.444
2.5	ψ(elev + village)p(.)	0.66	0.111	4	0.444 (0.111)	(0.241–0.614)	0.444
2.6	ψ(elev + village/road)p(.)	0.91	0.098	4	0.444 (0.113)	(0.220–0.611)	0.444
2.7	ψ(road)p(.)	1.35	0.078	3	0.444 (0.094)	(0.268–0.618)	0.444
2.8	ψ(elev + road)p(.)	1.38	0.077	4	0.444 (0.113)	(0.243–0.600)	0.443
2.9	ψ(village/forest edge)p(.)	1.85	0.061	3	0.444 (0.107)	(0.251–0.624)	0.443
2.10	ψ(elev)p(forest type)	2.46	0.045	4	0.444 (0.107)	(0.253–0.634)	0.443

ψ is the probability a site is occupied by sun bear and p is the detection probability where ψ(.)p(.) assumes that sun bear presence and detection probability are constant across sites. K is the number of parameters in the model, ΔAIC_c is the difference in AIC_c values between each model and ω_i is the AIC_c model weight. Sun bear occupancy estimates for both survey periods were not affected by spatial autocorrelation (Moran's $I = 0.03$, 0.01 respectively, $P > 0.1$).
SE, standard error.

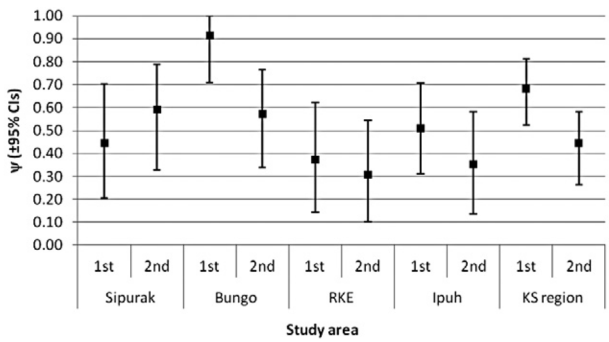

Figure 2 Temporal change in sun bear *Helarctos malayanus* occupancy across the Kerinci Seblat (KS) region and from four study areas conducted over a first (2004/06) and a second (2009/11) survey period. Ψ, the probability a site is occupied by sun bear; CIs, confidence intervals; RKE, Renah Kayu Embun.

95% CIs between the two survey periods overlapped (Fig. 2). This was further supported by the Wald test (Wald = 11.32, $Z = 1.83$, $P = 0.07$). At a finer scale, sun bear occupancy decreased by 37.5% at a rate of 9.4%year^{-1} over a 4-year survey period (Table 1) in Bungo, which experienced a higher rate of deforestation than the other study areas. Although the 95% CIs slightly overlapped between the two survey periods, the Wald statistic found this decrease to be significant (Wald = 15.64, $Z = 2.31$, $P = 0.02$), suggesting that Bungo experienced the greatest and fastest decline in occupancy compared with other study areas. Sun bear occupancy decreased in both Ipuh (31.1%) and RKE (17.2%) at rates of 7.8%year^{-1} and 2.9%year^{-1} over a 4-year and a 6-year survey period, respectively, but these trends were not significant. By contrast, occupancy increased by 32.4% at a rate of 6.5%year^{-1} over a 5-year survey period in Sipurak, but this trend was also not significant due to the relatively wide CIs (Fig. 2).

Our detectability models showed that, contrary to the 2004/06 survey period ($\beta_{forest\ type} \pm$ SE = –0.403 ± 0.451; Model 1.5), the primary forest type increased the probability of sun bear detectability in the 2009/11 survey period ($\beta_{forest\ type} \pm$ SE = 0.017 ± 0.501; Model 2.10), indicating a positive relationship between the density of large trees and detectability. Nevertheless, camera trapping resulted in relatively high detection probabilities (i.e. $P > 0.20$) for a species that is presumed hard to detect. Consequently, the occupancy models were able to distinguish reliably between sites with a low detection probability and sites where the species was absent, subsequently producing precise occupancy estimates (MacKenzie *et al*., 2002).

Discussion

This is the first study to attempt to measure spatio-temporal changes in sun bear populations in response to deforestation. Furthermore, it is one of the few studies to do so for a cryptic large-bodied mammal species living over extensive areas of rainforest in South-east Asia. Learning from our sampling design, it is recommended that future studies seek to increase the number of camera-trap placements and investigate the influence of different trap spacing distances on occupancy estimation and model precision. Moreover, sensor sensitivity may vary between different models of camera trap, thereby affecting detection probabilities. Consequently, future studies might also need to take the performance of different models of camera trap into account.

This study revealed that sun bear subpopulations inside KSNP, in areas experiencing lower levels of deforestation, remained relatively stable. The significant decline shown by the Bungo subpopulation is probably explained by its much higher deforestation rate. However, occupancy modelling must satisfy a number of important assumptions, one of which is independence between sampling sites (MacKenzie *et al*., 2002). This can be problematic for estimating occupancy of wide-ranging large-bodied mammal species. Large sampling sites, ideally the size of an individual's home range, are required to meet the independence assumption (Wibisono *et al*., 2011). Little is known about sun bear home-range size. Nevertheless, our sampling units were spaced at a minimum of 4 km based on a previous sun bear home-range data (Wong *et al*., 2004) and therefore considered to satisfy the this assumption. However, this subsequent increase in spacing resulted in the removal of data collected from an additional 57 (2004/06) and 46 (2009/11) camera traps operating in the four study areas. Future studies might investigate how to most efficiently use detection/non-detection data when trading off between camera-trap space distance and sample size. Our dataset was composed from various independent surveys targeted at smaller sections within the larger study area. Despite a good overall spatial coverage, the sampling was not random and so the overall estimate is not necessarily representative of the entire sun bear range.

Food availability often determines bear species habitat use and distribution. In Thailand, for example, sun bear signs, habitat use and behaviour were strongly influenced by fruit availability (Steinmetz *et al*., 2011). Therefore, sun bear detectability and occupancy may in turn be related to the density of fruiting trees. The detectability models (*p*(forest type)) revealed that contrary to the first survey period, sun bears had a higher detection probability in primary forests in the second survey period, possibly a result of higher fruit availability in this habitat. Furthermore, sun bear detection probability was higher in the second survey period regardless of the occupancy model. This further supports the relationship between sun bear detectability and density of fruiting trees, as fruit availability is likely to be lower in the second survey period as a result of forest clearance. Sun bears spend the majority of their time on the ground, preferring to feed on fallen fruits (G. Fredriksson. pers. comm.). Consequently, in areas of low fruit availability, sun bear detectability may increase due to more time spent travelling and foraging, while the overall occupancy decreases due to poor habitat.

Under natural conditions, lowland and hill forest types such as those in Bungo and Ipuh should support a higher productivity of fruiting trees. However, these lower elevation forests also experience higher deforestation rates (Linkie *et al*., 2008*b*) and are thus more likely to have food sources, such as the important dietary trees that occur in secondary forest, removed. Additionally, although camera trapping between the two survey periods was conducted over similar seasons, the supply of natural foods may nevertheless vary between months and years (van Schaik, Terborgh & Wright, 1993; Wong *et al*., 2005). Excluding food availability and abundance at sampling sites may be a limitation to this research, and therefore, future studies should consider measuring and modelling fruiting tree density.

Data from the Bungo study area suggest that sun bear subpopulation declines were linked to high rates of deforestation, the first time that such a relationship has been documented for this species. Given that future deforestation patterns are predicted to increase across the KS region (Linkie, Smith & Leader-Williams, 2004), it is likely that sun bear populations will continue to decline. Furthermore, across the KS region, the top models for sun bear occupancy from both survey periods were largely negatively influenced by threat proxies such as distance to roads and villages, indicating that sun bears are sensitive to human disturbances. Consequently, a robust law enforcement response, particularly in the lowland areas, would yield substantial benefits for this species (Linkie, Rood & Smith, 2010) by mitigating illegal encroachment past the KSNP border.

Given the rich biodiversity of Indonesia, which supports nearly 10% of the world's remaining tropical forest, its high rates of deforestation remain cause for concern among conservationists (Jepson *et al*., 2001; Whitten, Holmes & MacKinnon, 2001). If threatened large-bodied mammal populations are to be conserved in tropical landscapes, such as those in KSNP, management should concentrate on conserving the remaining forest habitat within protected areas and reviewing spatial land-use plans to clarify whether certain types of forest clearance outside of these areas are legal or as in the case of this study, illegal. For the KS region, and likely true for elsewhere in Sumatra, the key recommendation is the prosaic one of enforcing the rule of law both inside and outside of the protected area to prevent further illegal forest clearances. This does not appear to be happening, and deforestation in Sumatra's rainforests has now reached a crisis point. For example, KSNP has now been placed on UNESCO's World Heritage Site Danger List (UNESCO, 2011). Conservation management strategies for large protected areas such as KSNP are often limited by financial resources (Leader-Williams & Albon, 1988). Consequently, it is imperative to focus such strategies in areas of need for greatest effect and impact. Thus, the monitoring protocol developed in this study provides a valuable feedback mechanism for NP authorities to assess the cost-effectiveness of existing conservation strategies, particularly in tackling deforestation and in prioritizing future conservation action.

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