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Managing sun bears in a changing tropical landscape

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ABSTRACT

Aim Across the tropics, large-bodied mammal species are threatened by rapid and widespread forest habitat conversion by either commercial logging or agricultural expansion. How such species use these habitats is an important area of research for guiding their future management. The tropical forest-dwelling sun bear, *Helarctos malayanus*, is the least known of the eight bear species. Consequently, the IUCN/SSC Bear Specialist Group ranks research on this species as a top priority. This study aims to investigate landscape variables that influence sun bear habitat use in forests under varying levels of degradation and protection.

Location A 20,998 km^2 Sumatra forest landscape covering Kerinci Seblat National Park (KSNP), Batang Hari Protection Forest (BHPF) and neighbouring logging and agricultural concessions.

Methods An occupancy-based sampling technique using detection/non-detection data with 10 landscape covariates was applied in six study areas that operated a total of 125 camera traps. The potential differences between habitat use (ψ) of sun bears were first modelled with broad-scale covariates of study area, land-use types and forest type. Sun bear habitat use was then investigated with the finer-scale landscape features associated within these areas.

Results From 10,935 trap nights, sun bears were recorded at altitudes ranging from 365 to 1791 m. At a broad-scale, habitat use increased with protection status, being highest in KSNP (0.688 ± 0.092, ± SE) and BHPF (0.621 ± 0.110) compared to production (0.418 ± 0.121) and convertible (0.286 ± 0.122) forests. Within these areas, sun bears showed a preference for forest that was further from public roads and villages and at a lower elevation.

Main conclusions The habitat suitability model identified several high-quality habitat patches outside of the priority conservation areas for immediate protection. Consequently, conservation management strategies should emphasize the importance of high conservation value forests and prohibit further conversion of threatened lowland forests.

Keywords

Deforestation, habitat use, high conservation value forests, land-use planning, large mammal conservation, logging, plantation, Ursidae.

INTRODUCTION

Deforestation and unsustainable hunting in the tropics have degraded many landscapes to the point that they now no longer support viable populations of threatened species (Sodhi *et al.*, 2009; Bennett, 2011). Traditional approaches to conserving these landscapes and their wildlife populations have tended to focus on protected area management (IUCN, 1994; DeFries *et al.*, 2005). However, it is questionable whether the existing protected areas provide adequate habitat cover, quality or indeed protection for threatened species (Catullo *et al.*, 2008), as designation is often based on socio-economic and political priorities rather than assessments of wildlife habitat requirements (Margules & Pressey, 2000). This has, for example, led to significant sized patches of lowland tropical forests being excised from protected areas for commercial logging (Daily *et al.*, 2009).

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The threat posed by deforestation tends to disproportionately affect large-bodied mammals because of their large range requirements (Kinnaird *et al.*, 2003). Thus, to halt the ongoing loss of large-bodied mammal populations, identification of high conservation value areas is required (Hoffmann *et al.*, 2010), but the detailed information on the distribution of species required for this purpose is often lacking (Rondinini *et al.*, 2005). The requisite distributional data for developing conservation priorities, whilst available for many species in the form of regional range data (Rodrigues *et al.*, 2004), are less useful for conservation agencies that require finer-scale information, such as spatial distribution and use of habitat under varying levels of protection.

The sun bear is a large-bodied mammal species that historically ranged from India to Indonesia and China. Today, its range has contracted considerably. Sun bears are now patchily spread throughout much of this former range and have disappeared entirely from three of its 12 former range countries (Servheen, 1999). Agricultural expansion into forest habitat, especially on the islands of Indonesia and Borneo, and poaching for trade, especially in mainland Southeast Asia, are the primary drivers of this dramatic range and population reduction (Meijaard, 1999). The previously data deficient sun bear was recently reclassified by the International Union for Conservation of Nature (IUCN) as Vulnerable (IUCN, 2011). Yet, the conservation management of this species is hampered by a lack of basic, yet fundamentally important, ecological knowledge of habitat preferences and geographic distributions.

Sun bears have a varied diet (Wong *et al.*, 2002; Fredriksson *et al.*, 2006), which enables the species to live in a range of habitats (Linkie *et al.*, 2007). Previous research in the Kerinci Seblat (KS) region, which estimated sun bear occupancy from four different habitat types, showed that occupancy was highest in a primary–secondary hill forest and lowest in a primary submontane forest (Linkie *et al.*, 2007). However, given the rapid rates of forest conversion across the KS region (Linkie *et al.*, 2004; Uryu *et al.*, 2010), sun bear distribution and occupancy in these habitats are likely to change. Sun bear research has predominantly investigated habitat use within lowland forest reserves and protected areas (Servheen, 1999; Wong *et al.*, 2002, 2004; Fredriksson *et al.*, 2006). The value of higher elevation and unprotected forests for sun bears has therefore received little attention (Linkie *et al.*, 2007). This is a critical information gap because the disproportionately high and unyielding rates of deforestation in lower elevation forest are undoubtedly shaping the spatial distribution and habitat use patterns of sun bears, as well as other large-bodied mammal species, in the tropics (Kinnaird *et al.*, 2003; Wibisono *et al.*, 2011).

An important limitation for sun bear habitat management is poor land-use planning, with large forest areas of high biological value still being cleared for plantations or commercial logging, which uses unsustainable practices (Fitzherbert *et al.*, 2008). Comparative studies on the influence of different land-use types on the diversity and distribution of biodiversity, or components of it, are essential for policy makers and conservation managers (Gillison *et al.*, 2004). Here, we provide the first assessment of sun bear habitat use across a large tropical forest landscape in Sumatra that covers all of the main land-use types, ranging from strictly protected areas and conservation areas, production forests and forests that are classified as legally convertible to non-forest by Indonesian law, defined here as convertible forests. We investigated (1) sun bear habitat use at a broad-scale looking at protection status, (2) habitat use at a finer-scale within these study areas and (3) use the main findings to make broad recommendations for the conservation of sun bears, which should also apply to other large-bodied mammals, living in human-altered tropical landscapes.

METHODS

Study area

The west-central Sumatra region consists of several land-use types that include a protected area, Kerinci Seblat National Park (KSNP; 13,300 km^2); conservation area, Batang Hari Protection Forest (BHPF; 1,700 km^2); production forests (4,888 km^2) and convertible forests (1,110 km^2; Fig. 1a). This vast protected area network and diverse range of forest habitats should represent a stronghold for sun bears and other threatened species of large-bodied mammals (Holden *et al.*, 2003; Linkie *et al.*, 2006). However, with a mean deforestation rate across the region of 1.10%yr^{-1} (2004–2008/9; Uryu *et al.*, 2010), forest conversion into agricultural farmlands represents a significant threat.

This study focused on six camera trapping areas: two inside KSNP; two that straddled the KSNP border with placement also in convertible and/or production forests; one inside BHPF; and one inside an active logging concession bordering BHPF, referred to hereafter as PT-AMT (Fig. 1b; Table 1). This covered three of the eight mainland Sumatran provinces (Bengkulu, Jambi and West Sumatra) and all of the main tropical forest types in which sun bears are known to live, encompassing selectively logged and primary lowland/hill forest to pristine montane forests (Servheen, 1999). These six areas have different levels of forest degradation and protection status (Table 1).

Data collection

From February 2008 to April 2011, a detection/non-detection sampling technique using camera trap data was used to estimate sun bear habitat use in the KS region and its neighbouring forests. Between 18 and 23 camera traps were deployed in each area, resulting in a total of 125 camera trap placements across the west-central Sumatra project landscape (Table 1). A combination of film and digital infrared camera models was used including PhotoScout (PTC Technologies Inc, Boston, MA, USA), Moultrie (Moultrie^{TM}, Alabaster, AL, USA) and Bushnell (Bushnell Corporation, Overland

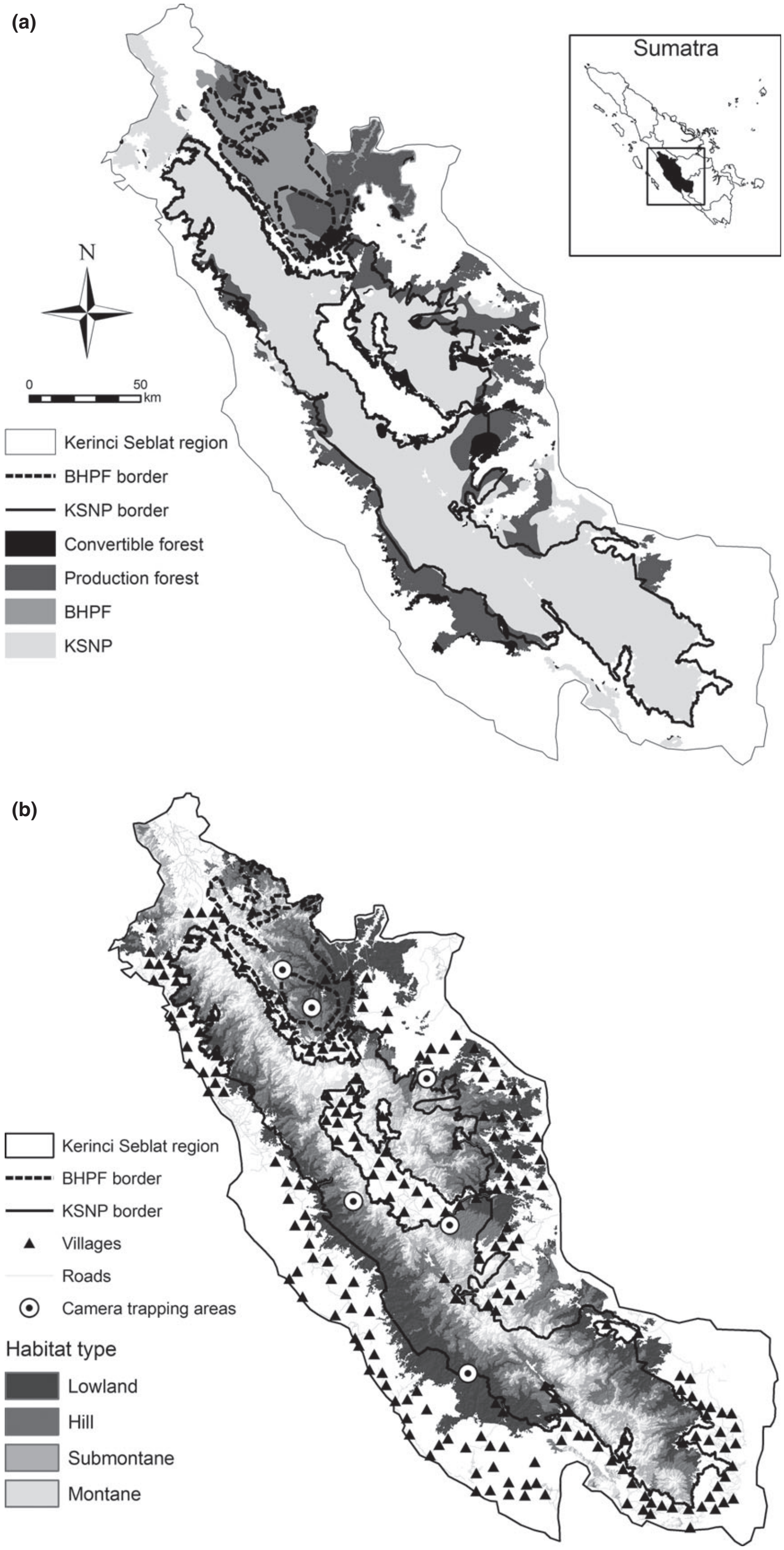

Figure 1 The west-central Sumatra project landscape covering Kerinci Seblat National Park (KSNP), Batang Hari Protection Forest (BHPF) and neighbouring forests, showing (a) the different land-use types, and (b) the location of camera trap study areas.

Park, KS, USA). Cameras were placed along ridge and animal trails at a height of approximately 0.5 m above the ground. To obtain a sufficient number of sampling sites at each study area, camera traps were spaced with a minimum distance of 2 km based on sun bear movement and home range data (Wong *et al.*, 2004). This camera spacing was to ensure that

Table 1 Camera trap study areas used for estimating sun bear habitat use in the west-central Sumatra project landscape

Study area	Number of camera traps	Camera trap area (km^2)	Altitudinal range (m)	Main habitat type and protection status	Camera trapping dates
PT-AMT	18	124	365–1022 (mean: 653)	Active logging concession bordering primary lowland/hill forest	Feb–May 2008
Batang Hari Protection Forest (BHPF)	21	165	340–1461 (mean: 742)	Primary hill/submontane forest bordering logging concession	June–Sept 2008
Kerinci Seblat National Park (KSNP)					
Sipurak	21	88	694–1254 (mean: 901)	Primary hill/submontane forest inside KSNP adjacent to ex-logging concession	Dec 2009–Mar 2010
Bungo	21	90	363–1630 (mean: 753)	Primary–secondary hill forest predominantly inside an ex-logging concession, with a few sites inside KSNP	Apr–July 2010
RKE	23	104	947–1941 (mean: 1194)	Primary submontane forest inside KSNP	Aug–Nov 2010
Ipuh	21	118	145–1032 (mean: 511)	Primary–secondary lowland forest predominantly inside an ex-logging concession, with a few sites inside KSNP	Nov 2010–Feb 2011

no sun bear within the sampling areas had a zero probability of being detected, thereby adhering to a critical assumption of the occupancy-based method used in this study (MacKenzie *et al.*, 2002). Cameras were active 24 h per day, set with a 1-min delay between exposures, programmed to record the time and date of each event and were active for approximately 90 days to avoid possible violation of the population closure assumption (Karanth & Nichols, 1998). Cameras were visited every 2 weeks to replace their film, memory cards and batteries, as well as to check their condition.

Quantification of landscape covariates

A dataset of 10 potential landscape variables that were thought to influence sun bear habitat use was constructed within ArcGIS v9.3 software (ESRI, Redlands, CA). The raw data were obtained from several sources: elevation and slope (Rabus *et al.*, 2003); the position of public roads, logging roads, rivers, villages and forest edge (Indonesian National Coordination Agency for Surveys and Mapping); land-use type (protected areas, forest reserves, production forests and convertible forests; WWF-Indonesia forest data); forest type (primary and degraded forest); and study area (PT-AMT, BHPF, Sipurak, Bungo, RKE and Ipuh). Elevation and slope covariates were extracted at a 30 × 30 m resolution, and a single value per site was obtained by averaging all the pixel values within each sampling site (camera trap placement). The spatial covariates of distance to public roads, logging roads, rivers, villages and forest edge (from within the forest) were calculated within ArcGIS v9.3 using the Spatial Analyst extension from each sampling site coordinate.

Statistical analysis and predictive model construction

The 10 landscape variables were categorized as being either broad-scale or fine-scale. Broad-scale variables included categorical covariates of land-use type, forest type and study area. Fine-scale variables included elevation, slope and distance to public roads, logging roads, rivers, villages and forest edge. The continuous landscape variable data extracted from each sampling site were imported into SPSS v.18.0 software (SPSS Inc., Chicago, IL, USA) and logarithmically transformed to reduce the likelihood of extreme values having a disproportionate influence on the overall dataset (Royston & Sauerbrei, 2007). To test for non-independence between covariates, a Spearman's rank correlation coefficient (r_s) was calculated between pairwise variables. Correlated covariates were combined using principal component analysis (Abdi & Williams, 2010), using the data reduction technique in SPSS v.18.0 software, to produce a single covariate that was then used in the final data analysis. The covariates of distance to public roads and villages ($r_s = 0.70$), distance to forest edge and villages ($r_s = 0.53$) and distance to logging roads and elevation ($r_s = 0.55$) were correlated ($P < 0.05$) and entered within unique combined covariates (i.e. Dist. public roads/villages; Dist. Forest edge/village; Dist. Logging/elevation). As different covariates can have different ecological effects, each correlated covariate was also modelled separately, but not in the same model. 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 the camera trap sampling unit coordinates by calculating Moran's I statistic.

This study applied a sampling design in which the number of camera trap sample sites (n) was visited multiple times on K sampling occasions. In turn, this allowed for inferences over sun bear habitat use, whilst accounting for imperfect detection, to be made. Detection/non-detection data were collected from camera trap surveys to obtain encounter histories for sun bears. The detection (1) or non-detection (0) sequence of sun bears over a 3-month trapping duration per study area was then recorded as a detection history. Within this detection history, the 3-month sampling period was divided into six consecutive 2-week sampling occasions. Detection histories for each of the six study areas were combined to produce one dataset containing a total of 125 sampling sites. The resulting detection history framework (n = 125, K = 6) was entered into PRESENCE v2.3 software (Hines, 2006).

Within the PRESENCE software, a two-stage logistic regression analysis was performed to determine which broad-scale factors (i.e. land-use type, study area and forest type) influenced sun bear habitat use (ψ) and then how several finer-scale factors explained habitat use within these study areas. Models included detection probability as a constant, $p(.)$, or as a function of site-specific covariates, p(covariate). Candidate models were ranked by their second-order information criterion (AIC_c) values, corrected for small sample sizes, and the Akaike weights (w_i; Burnham & Anderson, 2002). The Akaike weight represents the ratio of ΔAIC_c values for the whole set of candidate models, providing a strength of evidence for each model. The top-ranking candidate model was used to determine the sun bear habitat use for the west-central Sumatra project landscape. The corresponding beta (β) coefficients from the covariates in the top model, derived from PRESENCE software, were used to construct a predictive habitat suitability model (P) in ArcGIS v9.3 using the following equation:

$$P = \frac{1}{1 + e^{-\left(\beta_0 + \sum \beta_i X_i\right)}}$$

where β_0 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 predictive power of the habitat suitability model was validated using sun bear habitat use data that were derived from a separate camera trapping survey collected from February 2011 to May 2011. Subsequently, an additional 40 camera trap sampling sites were selected within KSNP. This was achieved by randomly selecting four forest areas along the KSNP border that varied in habitat type. A total of 10 camera traps were deployed within each area along animal and ridge trails with a spacing greater than 2 km apart to minimize spatial autocorrelation. Camera traps were left for a period of 1 month at each sampling site. Detection/non-detection data for each site were collected and entered into PRESENCE software to generate site-specific habitat use estimates. A Spearman's rank correlation coefficient was used to test for a correlation between model estimated values of habitat use and those generated by the independent dataset for each corresponding 90 m^2 suitability model pixel (Linkie *et al.*, 2006).

RESULTS

From February 2008 to April 2011, sun bears were camera trapped for a combined sampling effort of 10,935 trap nights comprising 1620 trap nights in PT-AMT, 1737 in BHPF, 2042 in Sipurak, 1762 in Bungo, 1884 in RKE and 1890 in Ipuh. Sun bears were detected in 47 of the 125 units, corresponding to a naïve occupancy estimate of 0.376. Individual sun bear records ranged in altitude from 365 m to 1791 m above sea level (a.s.l.).

Broad-scale patterns

At a broad-scale, sun bear habitat use was found to be strongly influenced by land-use type (Model 1.1; Table 2). Modelling land-use types as a function of sun bear habitat use produced the following beta coefficient values ($\beta_i \pm$ SE): $\beta_{KSNP} = 0.800 \pm 0.193$, $\beta_{BHPF} = -0.311 \pm 0.242$, $\beta_{production\ forest} = -1.12 \pm 1.03$ and $\beta_{conertible\ forest} = -1.70 \pm 1.33$. The positive beta regression coefficient for KSNP (protected area) indicates this land-use type increases the probability of habitat use by sun bears, whilst the negative beta regression coefficients for production and convertible forests imply the opposite. Consequently, sun bear habitat use ($\hat{\psi} \pm$ SE) was highest in the protected forests of KSNP (0.688 ± 0.092), followed by BHPF (0.621 ± 0.110), production forests (0.418 ± 0.121), and lowest in convertible forest (0.286 ± 0.122). However, modelling land-use types as a function of sun bear detection probability, p(land use), found no significant differences between production forests (0.391 ± 0.059; ±SE), BHPF (0.371 ± 0.117), convertible forests (0.322 ± 0.113) and KSNP (0.305 ± 0.050; Model 1.3, Table 2).

Fine-scale patterns

At a fine-scale, sun bear habitat use was best explained by distance to public roads/villages and elevation, and this model provided an adequate description of the data (Model 2.1; Table 2). The summed model weights for each factor with respect to habitat use were as follows: distance to roads/villages (78.3%) and elevation (51.7%). Sun bears showed a preference for forest that was located further away from public roads and villages and at lower elevations (Table 3). The corresponding estimated odd ratios for a one unit increase in each of the covariates, $\widehat{OR}_j = e^{\hat{\beta} j}$, were $\widehat{OR}_{\text{public roads/villages}}$ = 11.2 ± 0.05 and $\widehat{OR}_{\text{elevation}}$ = 0.16 ± 0.12. This final model was not affected by spatial autocorrelation (Moran's I = 0.03,

Table 2 Summary of model selection procedure for sun bear habitat use within 125 camera trap sites across the west-central Sumatra project landscape

Model no.	Model	K	ΔAIC_c	w_i	X^2	P-value	$\hat{c}$
Broad-scale analysis							
1.1	ψ(Land use)p(.)	3	0.00	0.472	66.97	0.726	0.81
1.2	ψ(Land use + Study area)p(.)	4	1.87	0.185	55.76	0.523	0.91
1.3	ψ(Land use + Study area)p(Land use)	5	2.14	0.162	56.98	0.519	0.85
1.4	ψ(Study area)p(.)	3	2.15	0.161	53.98	0.672	0.82
1.5	ψ(.)p(.)	2	6.40	0.019	59.46	0.648	0.83
Fine-scale analysis							
2.1	ψ(Dist. public roads/villages + elevation)p(.)	4	0.00	0.321	5.39	0.631	0.82
2.2	ψ(Dist. public roads/villages)p(.)	3	0.42	0.261	5.40	0.592	0.85
2.3	ψ(.)p(.)	2	1.80	0.131	5.38	0.620	0.84
2.4	ψ(Dist. public roads/villages + elevation)p(Dist. public roads/villages)	5	2.14	0.110	5.48	0.570	0.86
2.5	ψ(Dist. public roads/villages)p(Dist. public roads/villages)	4	2.52	0.091	5.39	0.621	0.82
2.6	ψ(Elevation)p(.)	3	2.64	0.086	5.56	0.547	0.86

ψ is the probability a site is occupied by a sun bear and p is the sun bear detection probability where ψ(.)p(.) assumes 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; w_i is the AIC_c model weight; X^2 is the test statistic for model fit; P-value is the probability of observing a test statistic $\geq X^2$ based on 999 parametric bootstraps; and $\hat{c}$ is the estimated overdispersion parameter.

Table 3 Logit models estimating sun bear habitat use, with beta (β) coefficient and standard error (SE) estimates for the top-ranked models (from Table 2)

Model no.	Model	$\beta_0^{(constant)} \pm$ SE	$\beta_1^{(Roads/villages)} \pm$ SE	$\beta_2^{(elevation)} \pm$ SE
2.1	ψ(Dist. public roads/villages + elevation)p(.)	14.732 ± 2.48	2.414 ± 0.55	−1.844 ± 0.78
2.2	ψ(Dist. public roads/villages)p(.)	7.530 ± 2.52	1.96 ± 0.63	–
2.3	ψ(.)p(.)	−0.332 ± 0.20	–	–
2.4	ψ(Dist. public roads/villages + elevation)p(Dist. public roads/villages)	14.834 ± 2.47	2.443 ± 0.55	−1.844 ± 0.78
2.5	ψ(Dist. public roads/villages)p(Dist. public roads/villages)	7.631 ± 2.52	1.988 ± 0.63	–
2.6	ψ(Elevation)p(.)	–	–	−1.226 ± 0.97

$P > 0.05$) and thus used to construct a predictive habitat suitability model.

The predictive habitat suitability model showed that sun bears predominantly used habitats within the KSNP border (Fig. 2). The proximity of public roads and villages to the forest areas outside KSNP reduced sun bear habitat suitability. Habitat quality in production and convertible forest areas was significantly lower than protected areas. The predicted values of sun bear habitat use were positively and significantly correlated with sun bear habitat use estimates that were derived from independent camera trap data ($n = 40$, $r_s = 0.557$, $P < 0.001$).

DISCUSSION

This study is the first to assess sun bear habitat use across a large tropical landscape. The predictive habitat suitability model revealed how increased human disturbances, indicated by the presence of public roads, villages and elevation, negatively influenced sun bear habitat use across the west-central Sumatra project landscape. Habitat use was predicted to be higher in protected areas than in forest reserves, production and convertible forests. Areas within the BHPF border ranked high in sun bear habitat use; however, the presence of public roads and villages surrounding the BHPF reduced its suitability. Whilst the World Heritage Site of KSNP was shown to be the most important area, its continuing good habitat status for sun bears is now uncertain since its recent placement on the UNESCO Danger List due to the high levels of illegal logging and agricultural encroachment (UNESCO, 2011).

Modelling sun bear habitat use

This study demonstrates the use of a suitable and accurate method to model habitat suitability for sun bears and indeed other threatened large-bodied mammals that have proved a challenge to study in the wild. The detection/non-detection sampling framework accounts for imperfect detection (MacKenzie *et al.*, 2002) and allows for a number of predictor variables to be included, providing inferences about the factors influencing sun bear habitat use across multiple scales (Gray *et al.*, 2010). Consequently, this method modelled with environmental covariates resulted in a habitat suitability model with a strong predictive power, as tested by the separate camera trap survey. However, as

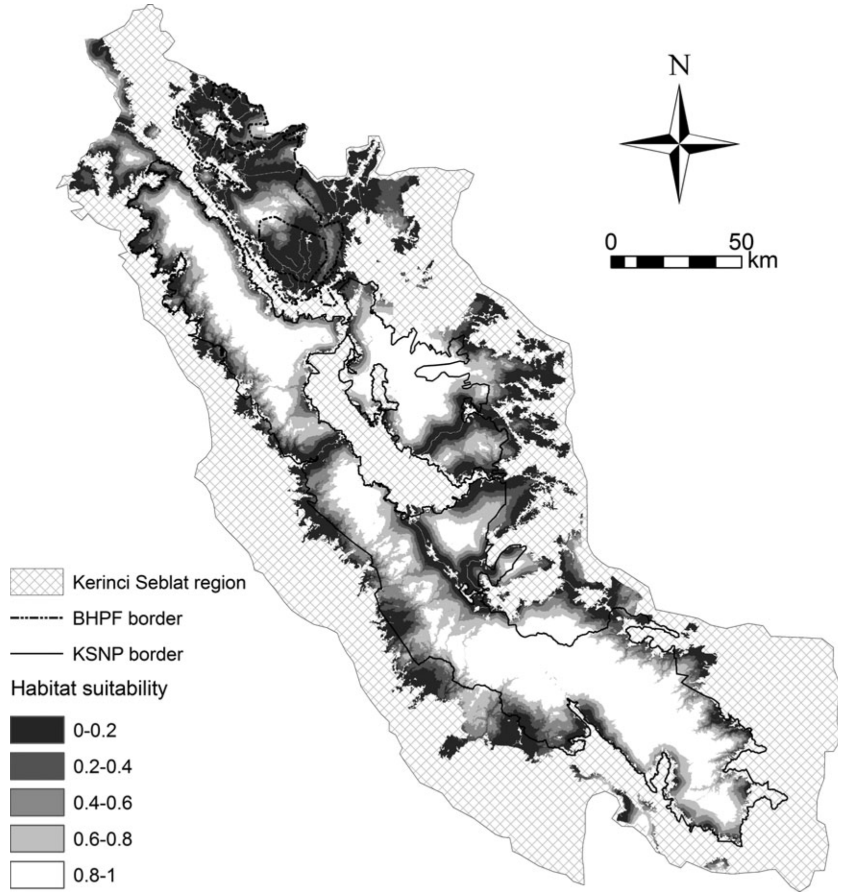

Figure 2 Sun bear habitat suitability in west-central Sumatra covering Kerinci Seblat National Park (KSNP), Batang Hari Protection Forest (BHPF) and neighbouring forests.

the occupancy-based sampling method relies on temporal closure of species populations during the survey period, this modelling assumption can put severe restrictions on the practicality of using occupancy to model species habitat suitability.

Sun bears, and large-bodied mammal species in general, often focus habitat use in areas where food resources are abundant (Schoen, 1990; Nomura & Higashi, 2000; Steinmetz *et al.*, 2011). This foraging behaviour is often referred to as the Ideal Free Distribution (IFD) theory, where species distribution is proportional to resource availability (Fretwell & Lucas, 1970). A key insight into the IFD theory is that as the density of individuals on a habitat patch increases, the suitability of that patch then decreases. Consequently, sun bear habitat use across the west-central Sumatra region may be dependent on the species occupancy state in certain habitat types. However, this theory has often been disproved in experimental studies. For example, black bears, *Ursus americanus*, have been shown not to conform to the IFD theory but rather to the Ideal Despotic Distribution theory where subordinate individuals are constrained in their choice of area by dominant individuals (Beckmann & Berger, 2003). Furthermore, the IFD theory relies on a set of assumptions, one of which is that resource quality of each habitat patch does not change over time (Fretwell & Lucas, 1970), which is an unlikely explanation for sun bear habitat use in the Sumatra landscape. Food availability is likely to be higher in lower elevation forests. However, logging activities and agricultural expansion in these habitats can affect sun bear habitat use by altering foraging patterns. These human disturbances can prevent access to productive forage areas, reduce the abundance of key resources and alter fruit productivity, availability and distribution. Consequently, the predictive sun bear habitat suitability model derived from detection/non-detection data does not describe core sun bear ecological niche characteristics but rather represents an adaptation to local conditions. This result is likely to be influenced by habitats that are highly fragmented, such as those found across the KS region and neighbouring forests.

Sun bear habitat use derived from the detection/non-detection data revealed that sun bears used a wide range of habitat types, but more fully use submontane and montane regions ($\psi \geq 0.9$). As a result, these habitat types can be interpreted as suitable for sun bears. Consequently, management recommendations based on these findings should be treated with some caution. These habitat types still need to be considered against their relative importance because sun bear abundance will vary in these forest types. For example, previous studies have shown the importance of lowland forests < 500 m a.s.l. (Servheen, 1999; Wong *et al.*, 2002, 2004; Steinmetz *et al.*, 2011), where food productivity is higher

(Steinmetz *et al.*, 2011). It is likely that some of the factors, for example, accessibility, that are driving forest loss across west-central Sumatra also influence sun bear habitat use in a similar way (Linkie *et al.*, 2008). Thus, the fine-scale model may have been indirectly testing for forest loss, by incorporating factors that are related to accessibility, within the habitat use model. Additionally, this study only obtained sun bear data of altitudes up to 1791 m a.s.l. but the predictive habitat suitability model extrapolated high-quality habitat into higher elevation forests (montane forests). Despite these areas having low human disturbances, vegetation is scarce. Subsequently, predictions of sun bear habitat use in montane forests over this elevation cannot be reliably made.

The habitat suitability model developed in this study was based on 47 sites with detections and 78 sites without detections. A greater number of sampling sites would have been preferable; however, with a significant sampling effort of 10,935 trap nights over a wide geographic coverage, the detection/non-detection data may give an adequate representation of the sun bear distribution across the entire study area.

Implications for sun bear conservation management

Most of the lowland forests in the KS region are being cleared by illegal logging and agricultural expansion (Jepson *et al.*, 2001; Linkie *et al.*, 2004), which remove large fruiting trees and other food sources that are predicted to influence sun bear detection (Steinmetz *et al.*, 2011). However, as there was no significant difference between sun bear detection probability in different land-use types, it is likely that sun bears still use landscapes deemed unsuitable by the predictive habitat suitability model, that is, production and convertible forests. Yet, their predicted habitat use in these landscapes is a reflection of these areas having been degraded. The higher probabilities of sun bear habitat use in protected forest areas, particularly at higher elevations, may be an artefact of forest clearance (Rood *et al.*, 2010). Deforestation patterns have altered the suitability of lowland forests through their rapid and widespread conversion to poorer quality habitat types, that is, production and convertible forests.

Sun bears are more likely to use undisturbed lowland forests that have higher fruit productivity than higher elevation forests (Steinmetz *et al.*, 2011). Previous sun bear studies have also shown that sun bear occupancy was significantly higher in degraded lowland forests than in primary montane forests (Linkie *et al.*, 2007), indicating that these degraded lowland habitats potentially offer better quality habitat than higher elevation forests. Subsequently, conservation strategies should be aimed at protecting the remaining lowland forests thus preserving suitable habitat for sun bears.

Sun bears are predicted to use most of the forest inside KSNP, except in those areas where public roads enter the National Park, which reduces habitat quality. However, a recent study assessed the trends of four sun bear subpopulations in and around KSNP (Wong *et al.*, in press). Over the seven-year monitoring period, the two subpopulations inside KSNP remained stable, whilst another showed signs of an increase. In contrast, the subpopulation located outside of KSNP, and in the area with the highest levels of deforestation, underwent a significant decline.

In the past, there has been a lack of biological knowledge in land-use planning in Sumatra, which has hindered the conservation of large-bodied mammals through rapid and unmitigated agricultural expansion. However, through the recognition of the current state of Indonesia's forests, district and provincial governments are starting to integrate ecosystem services and biodiversity in their respective land-use plans (Barano *et al.*, 2010). One approach that promotes the sustainable development of agriculture whilst accounting for the conservation of biodiversity and habitat is the High Conservation Value Forest (HCVF) approach (Jennings, 2004). The HCVF approach is now being used as a criterion for sustainable production in some of the fastest expanding agricultural plantation crops (Dennis *et al.*, 2008). In particular, the Roundtable of Sustainability Palm Oil has adopted the HCVF approach, making it a cornerstone of their sustainability standard. However, there are a number of critical weaknesses to the HCVF approach (Yaap *et al.*, 2010). One such weakness of the approach is that the quality and accuracy of assessments are dependent on the practitioner, so greater accuracy in methodologies and reporting is needed. This study identified several high-quality patches outside the borders of KSNP for immediate protection. The predictive habitat suitability model developed in this study can therefore provide an accurate and cost-effective framework for HCVF assessments that will promote the conservation of sun bears and other large-bodied mammals across a large landscape. Consequently, for effective conservation of large-bodied mammal species, priorities should be focused in areas of high habitat suitability through better protection and management (Sunarto *et al.*, 2012).

Determining the effect of land-use types on the habitat use of large-bodied mammals is an important indicator that can be used to address the reassessment of land-use plans and should be used in compliance with future spatial plans (Rood *et al.*, 2010). To conserve sun bears and other threatened large-bodied mammals, conservation management strategies should include better definition and management for existing production and convertible forest areas, such as increasing productivity within these areas instead of expanding, establishment of protective forest buffer zones to maintain crucial elements of the landscapes and reintegration of degraded landscapes back into protected areas, whilst emphasizing the importance of HCVF and prohibiting further conversion of threatened forests.

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REFERENCES

Abdi, H. & Williams, L. (2010) Principal component analysis. *Computational Statistics*, **2**, 433–459.

Barano, T., McKenzie, E., Bhagabati, N., Conte, M., Ennaanay, D., Hadian, O., Olwero, N., Tallis, H., Wolny, S. & Ng, G. (2010) Integrating Ecosystem Services into Spatial Planning in Sumatra, Indonesia. http://www.TEEBweb.org. Accessed on 28 December 2011.

Beckmann, J.P. & Berger, J. (2003) Using black bears to test ideal-free distribution models experimentally. *Journal of Mammalogy*, **84**, 594–606.

Bennett, E.L. (2011) Another inconvenient true: the failure of enforcement systems to save charismatic species. *Oryx*, **45**, 476–479.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodal inference: a practical information-theoretic approach*, 2nd edn. Springer-Verlag, New York.

Catullo, G., Masi, M., Facucci, A., Maiorano, L., Rondinini, C. & Boitani, L. (2008) A gap analysis of Southeast Asian mammals based on habitat suitability models. *Biological Conservation*, **141**, 2730–2744.

Daily, G.C., Polasky, S., Goldstein, J., Kareiva, P.M., Mooney, H.A., Pejchar, L., Ricketts, T.H., Salzman, J. & Shallenberger, R. (2009) Ecosystem services in decision making: time to deliver. *The Ecological Society of America*, **7**, 21–28.

DeFries, R., Hansen, A., Newton, A.C. & Hansen, M.C. (2005) Increasing isolation of protected areas in tropical forests over the past twenty years. *Ecological Applications*, **15**, 19–26.

Dennis, R. A., Meijaard, E., Nasi, R. & Gustafsson, L. (2008) Biodiversity conservation in Southeast Asian timber concessions : a critical evaluation of policy mechanisms and guidelines. *Ecology and Society*, **13**, 1–17.

Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Bruhl, C.A., Donald, P.F. & Phalan, B. (2008) How will oil palm expansion affect biodiversity? *Trends in Ecology and Evolution*, **23**, 538–545.

Fredriksson, G.M., Wich, S.A. & Trisno. (2006) Frugivory in sun bears (Helarctos malayanus) is linked to El Niño-related fluctuations in fruiting phenology, East Kalimantan, Indonesia. *Biological Journal of the Linnean Society* **89**, 489–508.

Fretwell, S.D. & Lucas, H.L. (1970) On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, **19**, 16–36.

Gillison, A.N., Liswanti, N., Budidarsono, S., van Noordwijk, M. & Tomich, T.P. (2004) Impacts of cropping methods on biodiversity in coffee agroecosystems in Sumatra, Indonesia. *Ecology and Society*, **9**, 1–31.

Gray, T.N.E., Phan, C. & Long, B. (2010) Modelling species distribution at multiple spatial scales: gibbon habitat preferences in a fragmented landscape. *Animal Conservation*, **13**, 324–332.

Hines, J.E. (2006) PRESENCE2 – Software to Estimate Patch Occupancy and Related Parameters. USGS – PWRC, Laurel, MD.

Hoffmann, M., Hilton-Taylor, C., Angulo, A. *et al.* (2010) The impact of conservation on the status of the world's vertebrates. *Science*, **330**, 1503–1509.

Holden, J.A., Yanuar, A. & Martyr, D.J. (2003) The Asian tapir in Kerinci Seblat National Park, Sumatra: evidence collected through photo-trapping. *Oryx*, **37**, 34–40.

IUCN. (1994) *Guidelines for protected area management categories*. IUCN, Gland, Switzerland and Cambridge, UK.

IUCN. (2011) 2011 IUCN Red List of Threatened Species. Available at: <http://www.iucnredlist.org.> Accessed on 21 October 2011.

Jennings, S. (2004) *HCVF for conservation practitioners*. Pro-Forest, Oxford, UK.

Jepson, P., Jarvie, J.K., MacKinnon, K. & Monk, K.A. (2001) The end for Indonesia's lowland forests? *Science*, **292**, 859–861.

Karanth, K.U. & Nichols, J.D. (1998) Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, **79**, 2852–2862.

Kinnaird, M.F., Sanderson., E.W., O'Brien., T.G., Wibisono, H.T. & Woolmer, G. (2003) Deforestation trends in a tropical landscape and implications for endangered large mammals. *Conservation Biology*, **17**, 245–257.

Linkie, M., Smith, R.J. & Leader-Williams, N. (2004) Mapping and predicting deforestation patterns in the lowlands of Sumatra. *Biodiversity and Conservation*, **13**, 1809–1818.

Linkie, M., Chapron, G., Martyr, D.J., Holden, J. & Leader-Williams, N. (2006) Assessing the viability of tiger subpopulations in a fragmented landscape. *Journal of Applied Ecology*, **43**, 576–586.

Linkie, M., Dinata, Y., Nugroho, A. & Hadir, I.A. (2007) Estimating occupancy of a data deficient mammalian species living in tropical rainforests: sun bears in Kerinci Seblat region, Sumatra. *Biological Conservation*, **137**, 20–27.

Linkie, M., Haidir, I.A., Nugroho, A. & Dinata, Y. (2008) Conserving tigers Panthera tigris in selectively logged Sumatran forests. *Biological Conservation*, **141**, 2410–1415.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.

Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.

Meijaard, E. (1999) Human-imposed threats to sun bears in Borneo. *Ursus*, **11**, 185–192.

Nomura, F. & Higashi, S. (2000) Effects of food distribution on the habitat usage of a female brown bear *Ursus arctos yesoenis* in a beach-forest zone of northernmost Japan. *Ecological Research*, **15**, 209–217.

Rabus, B., Eineder, M., Roth, A. & Bamler, R. (2003) The shuttle radar topography mission – a new class of digital elevation models acquired by spaceborne radar. *Journal of Photogrammetry and Remote Sensing*, **57**, 241–262.

Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I. *et al.* (2004) Effectiveness of the global protected are network in representing species diversity. *Nature*, **428**, 640–643.

Rondinini, C., Stuart, S. & Boitani, L. (2005) Habitat suitability models and the shortfall in conservation planning for African vertebrates. *Conservation Biology*, **19**, 1488–1497.

Rood, E., Ganie, A.A. & Nijman, V. (2010) Using presence-only modelling to predict Asian elephant habitat use in a tropical forest landscape: implications for conservation. *Diversity and Distributions*, **16**, 975–984.

Royston, P. & Sauerbrei, W. (2007) Improving the robustness of fractional polynomial models by preliminary covariate transformation: a pragmatic approach. *Computational Statistics and Data Analysis*, **51**, 4240–4253.

Schoen, J.W. (1990) Bear habitat management: a review and future perspective. *International Conference on Bear Research and Management*, **8**, 143–154.

Servheen, C. (1999) Sun bear conservation action plan. *Bears. Status survey and conservation action plan* (ed. by C. Servheen, S. Herrero and B. Peyton), pp. 219–223. IUCN, Gland, Switzerland and Cambridge.

Sodhi, N.S., Lee, T.M., Koh, L.P. & Brook, B.W. (2009) A meta-analysis of the impact of anthropogenic forest disturbance on Southeast Asia's Biotas. *Biotropica*, **41**, 103–109.

Steinmetz, R., Garshelis, D.L., Chutipong, W. & Seuaturien, N. (2011) The shared preference niche of sympatric Asiatic black bears and sun bears in a tropical forest mosaic. *PLoS ONE*, **6**, 1–11.

Sunarto, S., Kelly, M.J., Parakkasi, K., Klenzendorf, S., Septayuda, E. & Kurniawan, H. (2012) Tigers need cover: multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. *PLoS ONE*, **7**, 1–14.

UNESCO, 2011. World Heritage Convention. Available at: http://www.whc.unesco.org. Accessed on 15 October 2011.

Uryu, Y., Putrastuti, E., Laumonier, Y., Sunarto, Setiabudi., Budiman, A., Yulianto, K., Sudibyo, A., Hadian, O., Kosasih, D.A. & Stuwe, M. (2010) *Sumatra's Forests, their Wildlife and the Climate – Windows in Time: 1985, 1990, 2000 and 2009*. WWF-Indonesia Report, Jakarta.

Wibisono, H.T., Linkie, M., Guillera-Arroita, G. *et al.* (2011) Population Status of a Cryptic Top Predator: an Island-Wide Assessment of Tigers in Sumatran Rainforests. *PLoS ONE*, **6**, 1–6.

Wong, S.T., Servheen, C. & Ambu, L. (2002) Food habits of Malayan sun bears in lowland tropical forests of Borneo. *Ursus*, **13**, 127–136.

Wong, S.T., Servheen, C.W. & Ambu, L. (2004) Home range, movement and activity patterns, and bedding sites of Malayan sun bears *Helarctos malayanus* in the rainforest of Borneo. *Biological Conservation*, **119**, 169–181.

Wong, W-M., Leader-Williams, N. & Linkie, M. (in press) Quantifying changes in sun bear distribution and their forest habitat in Sumatra. *Animal Conservation*.

Yaap, B, Struebig, M.J., Paoli, G. & Koh, L.P. (2010) Mitigating the biodiversity impacts of oil palm development. *Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources*, **19**, 1–11.

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