Predicted distribution of the Sunda clouded leopard Neofelis diardi (Mammalia: Carnivora: Felidae) on Borneo

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Predicted distribution of the Sunda clouded leopard *Neofelis diardi* (Mammalia: Carnivora: Felidae) on Borneo

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Wilting et al. (2016: Table 2) list all co-authors' affiliations.

Abstract. The Sunda clouded leopard *Neofelis diardi* is a medium sized (15–25 kg) cat, found only on the Sundaic islands of Borneo and Sumatra. In recent years intensive camera-trapping surveys in Borneo have begun to shed light on the habitat associations and basic ecology of this elusive wild cat, but its distribution on an island-wide scale remains very poorly known. Such information is an essential element in the assessment of the Sunda clouded leopard's conservation status and in the development of conservation action. In this paper we use MaxEnt niche distribution modelling to make predictions regarding the current distribution of this cat on Borneo. We collected a total of 259 occurrence records for the Sunda clouded leopard, stemming from all Bornean regions apart from Brunei and South Kalimantan, of which 48 (Balanced Model) or 94 (Spatial Filtering Model) were used in our modelling. Our habitat suitability model suggests that this species has a widespread distribution over a large contiguous portion of Borneo. The only exception is South Kalimantan, which is predicted largely to comprise unsuitable habitat. The predicted distribution closely follows the current distribution of little-encroached forest on Borneo (including selectively logged and unlogged areas). The species is notably predicted to be absent from the extensive areas of oil palm plantation, particularly in much of the low-lying coastal land. The predicted range encompasses a large proportion of the existing and proposed protected area network on Borneo. We highlight the priority areas for the conservation of the Sunda clouded leopard in Borneo based on our predicted distribution.

Key words. Borneo Carnivore Symposium, Brunei, conservation priorities, habitat suitability index, Indonesia, Malaysia, species distribution modelling, survey gaps

Abstrak (Bahasa Indonesia). Macan Dahan adalah jenis kucing liar yang berukuran sedang (15–25 kg) yang hanya ditemukan di Dataran Sunda seperti Borneo dan Sumatera. Dalam beberapa tahun terakhir, survey intensif menggunakan kamera trap telah mulai menjelaskan asosiasi habitat dan ekologi dasar jenis kucing liar ini, tetapi data sebaran jenis ini pada skala keseluruhan pulau masih sangat kurang. Informasi tersebut merupakan informasi penting untuk menilai status konservasi Macan Dahan dan untuk mengembangkan aksi konservasi yang diperlukan. Dalam penelitian ini kami menggunakan pemodelan sebaran niche MaxEnt untuk membuat prediksi sebaran kucing liar ini di Borneo. Secara keseluruhan kami mengumpulkan 259 catatan kehadiran Macan Dahan di Borneo yang berasal dari Brunei hingga Kalimantan Selatan, dimana 48 (Model Penyeimbang) dan 94 (Model Spasial Tersaring digunakan dalam pemodelan. Hasil analisis pemodelan kesesuaian habitat menunjukkan bahwa jenis ini memiliki sebaran yang luas di Borneo. Satu-satunya pengecualian untuk daerah Kalimantan Selatan yang sebagian besar diprediksi tidak sesuai untuk habitat. Prediksi sebaran jenis ini meliputi sebagian besar kawasan lindung dan kawasan yang diusulkan sebagai kawasan lindung di Borneo. Berdasarkan prediksi distribusi, kami menyusun kawasan prioritas untuk konservasi Macan Dahan di Borneo.

Abstrak (Bahasa Malaysia). Harimau Dahan Sunda *Neofelis diardi* adalah kucing liar yang sederhana besar (15–25 kg). Ia hanya dijumpai di Borneo dan Sumatra di kepulauan Sunda. Sejak beberapa tahun kebelakangan ini, pemantauan yang intensif dengan menggunakan perangkap kamera di Borneo mula memberi maklumat tentang perkaitan habitat dan ekologi asas kucing liar yang sukar ditemui ini; tetapi pengetahuan tentang taburan kucing ini di Borneo masih sangat sedikit yang diketahui. Maklumat taburan ini merupakan elemen penting untuk menilai status pemuliharaan harimau dahan dan bagi pembentukan pelan pemuliharaan spesis ini. Dalam kajian ini, kami menggunakan pendekatan model taburan ceruk (niche) MaxEnt untuk membuat ramalan berkenaan taburan terkini harimau dahan di Borneo. Kami mengumpulkan sejumlah 259 rekod penemuan Harimau Dahan Sunda dari seluruh bahagian Borneo kecuali dari Brunei dan Kalimantan Selatan di mana 48 (Model Seimbang) dan 94 (Model yang ditapis secara spasial) rekod sesuai digunakan untuk tujuan pembentukan model. Model kesesuaian habitat kami menunjukkan bahawa Harimau Dahan Sunda mempunyai taburan yang meluas di sebahagian besar Borneo dengan pengecualian di Kalimantan Selatan, yang diramalkan sebahagian besarnya terdiri daripada habitat yang tidak sesuai untuk spesis ini. Taburan yang diramal ini menyamai taburan hutan terkini yang masih berada dalam keadaan baik di Borneo (termasuk hutan yang dibalak secara terpilih dan hutan yang belum dibalak), dan spesis ini diramalkan tidak terdapat di kawasan ladang kelapa sawit yang luas terutamanya di kawasan tanah rendah pesisiran pantai.

Ramalan taburan spesis ini merangkumi sebahagian besar jaringan kawasan perlindungan yang sedia ada dan dicadangkan di Borneo. Kami menyenaraikan kawasan-kawasan yang penting bagi pemuliharaan Harimau Dahan Sunda di Borneo berdasarkan ramalan taburan yang kami perolehi.

INTRODUCTION

The Sunda clouded leopard *Neofelis diardi* (Cuvier), is a medium sized (15–25 kg) cat, found only on the Sundaic islands of Borneo and Sumatra. Highly secretive and difficult to study, compared with other members of the subfamily Pantherinae (Pocock), the Sunda clouded leopard (Fig. 1) has received less research effort (Brodie, 2009) and consequently much of its biology remains unknown. Genetic (Buckley-Beason et al., 2006; Wilting et al., 2007, 2011) and morphological studies (Kitchener et al., 2006, 2007; Christiansen, 2008, 2009) have led to the recognition that this species is distinct from its mainland congener, the mainland clouded leopard *N. nebulosa* (Griffith), and that the two island forms are sufficiently distinct to warrant subspecies status: *N. d. diardi* in Sumatra and *N. d. borneensis* Wilting, in Borneo (Wilting et al., 2011).

Recent camera-trapping suggests that, on Borneo, the Sunda clouded leopard is primarily nocturnal, although also active during the day (Ross et al., 2010, 2013; Cheyne & Macdonald, 2011; Bernard et al., 2013; Hearn et al., 2013). There have been no studies of its diet preferences, but field observations suggest that its prey is diverse and includes terrestrial birds, porcupines (Gordon & Stewart, 2007), primates (Yeager, 1991; Matsuda et al., 2008; Morino, 2010) and ungulates (Davis, 1962; Rabinowitz et al., 1987; Bernard et al., 2012). Camera-trap data from multiple sites across Sabah showed that bearded pigs *Sus barbatus* Müller, exhibited greater nocturnal activity in the absence of Sunda clouded leopards, with female and young pigs showing the strongest response (Ross et al., 2013); this suggests that female and young pigs, in particular, might be key prey for the Sunda clouded leopard and are capable of altering their activity pattern in response to this predation risk. Typically, pantherine cats kill small prey with a powerful nape bite which severs or otherwise damages the spine, whereas large preys are usually dispatched with a suffocating throat bite (e.g., Karanth & Sunquist, 2000). Clouded leopards possess an enlarged gape and hypertrophied upper canines, which are more laterally compressed, or bladelike, in the Sunda clouded leopard (Christiansen, 2006, 2008). Christiansen (2006) speculated that such adaptations might facilitate nape-killing of large prey, but cautioned that further research, and particularly field observations, are needed before conclusions may be drawn.

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Fig. 1. A male Sunda clouded leopard *Neofelis diardi* photographed at around 1300 m a.s.l. in the Crocker Range Park, Sabah, Malaysia, on 23 October 2011. Image copyright AJ Hearn, J Ross & DW Macdonald.

The spatial ecology of this wild cat is largely unknown. A female in Sabah occupied a home-range of 16.1 km^2 and a core-range of 5.4 km^2 (95% and 50% fixed-kernel estimators, respectively) over a 109-day period (Hearn et al., 2013). Annual ranges, and those of males, are likely to be significantly larger.

The habitat associations and distribution of the Sunda clouded leopard on Borneo remain poorly known. It appears to be an adaptable yet rare species, being found in both primary and selectively logged dipterocarp forest, peat-swamp forest and mangroves, and at densities ranging from 0.8 to 4.4 individuals per 100 km^2 (Brodie & Giordano, 2012; Wilting et al., 2012; Cheyne et al., 2013; AJ Hearn, J Ross & DW Macdonald, unpublished data; B Loken et al., unpublished data). While the Sunda clouded leopard appears able to use some modified habitats, full effects of anthropogenic disturbance on its abundance and distribution remain unclear. Initial studies suggest that oil palm plantations might not readily be used (Ross et al., 2010; Bernard et al., 2012, 2014; Yue et al., 2015), but that they might not necessarily form a hard barrier to the species's movements (Nájera et al., 2013; AJ Hearn, J Ross & DW Macdonald, unpublished data). Wilting et al. (2006) listed the protected areas and commercial forest reserves in Sabah known to support Sunda clouded leopards.

Globally, The IUCN Red List of Threatened Species lists the Sunda clouded leopard as Vulnerable, and the Bornean subspecies as Endangered (Hearn et al., 2008a, b). Population density estimates of the species on Borneo, derived from targeted camera-trap surveys across a range of forest types and elevations, and a gradient of disturbance, range from 0.8 to 4.4 individuals per 100 km^2 (Brodie & Giordano, 2012; Wilting et al., 2012; Cheyne et al., 2013; AJ Hearn, J Ross and DW Macdonald, unpublished data; B Loken et al., unpublished data). A large proportion of surveys (six of 10) estimated fewer than 1.9 individuals per 100 km^2. Some camera-trap surveys on Borneo, specifically undertaken to detect and estimate the density of this species, failed to find it at all, including in the Kabili–Sepilok Forest Reserve, Sabah (AJ Hearn, J Ross and DW Macdonald, unpublished data) and at several forest sites in Kalimantan (Cheyne et al., in prep.), suggesting that Sunda clouded leopard presence across the forested landscape of Borneo might be somewhat patchy.

The greatest threat to the species is likely to stem from habitat loss and fragmentation through commercial logging and conversion to oil palm plantations. A recent analysis predicts that by 2020, 37% of the remaining forest on Borneo will have a greater than 25% risk of being deforested (Macdonald et al., in prep), resulting in both an outright loss of habitat and also the fragmentation of that remaining. In a modelling analysis of the likely impacts of this change on the Sunda clouded leopard, Macdonald et al. (submitted) predicted that between 2010 and 2020 the percentage of the landscape connected sufficiently for the species's dispersal in Borneo will decrease by over 60%: this could lead to both a large direct decline in the species's numbers and also a significant reduction in the potential gene flow between populations. Such fragmentation of habitat might also increase some populations' risk of disease through exposure to pathogens present in feral cat and dog populations. One study in Sabah found seropositive findings for canine parvovirus and/or distemper virus in feral cats and dogs, Malay civets *Viverra tangalunga* Gray, and common palm civets *Paradoxurus hermaphroditus* (Pallas), living sympatrically with Sunda clouded leopards (Nájera et al., in prep.).

Poaching of Sunda clouded leopard and/or hunting of its prey poses a significant threat island-wide, but the level of threat is likely to vary in intensity across the species's range as a result of differential hunting pressure (Rabinowitz et al., 1987; Bennett et al., 2000; Bennett & Gumal, 2001; Wilting et al., 2006; Cheyne et al., 2013; D'Cruze & Macdonald, 2015). Although the impact of such activities on the Sunda clouded leopard is poorly understood, the large potential overlap in species targeted by hunters and Sunda clouded leopards means that exploitative competition is probably suppressing population densities below carrying capacity. Indeed, a survey of hunting patterns in communities in Sabah and Sarawak between 1993 and 1995 showed that bearded pig, sambar *Rusa unicolor* (Kerr), and muntjacs *Muntiacus* Rafinesque, all shown to be prey species of Sunda clouded leopard, were favoured quarry, collectively comprising 82.8% and 96.6% of the dressed weight of animals hunted, in Sarawak and Sabah, respectively (Bennett et al., 2000). In the same study, as hunting pressure increased, the abundance of primates, hornbills (Bucerotidae Rafinesque), sambar, muntjacs and bearded pig all decreased, sometimes to local extirpation of large animals in areas of high hunting pressure (Bennett et al., 2000).

The Sunda clouded leopard is afforded protection throughout the Bornean range states. Collection and/or hunting are prohibited in Sabah, Sarawak, Brunei and throughout Kalimantan (as *N. nebulosa*), under the Sabah Wildlife Conservation Enactment (1997), Sarawak Wild Life Protection Ordinance (1998), Brunei Wildlife Protection Act 1978, and the Appendix of The Government of Republic of Indonesia Regulation No. 7 (1999), respectively. The species is presumably listed on CITES Appendix I, to which all three range countries are parties, and thus sufficient legislation is in place theoretically to control international trade. When *N. nebulosa* was originally placed on Appendix I, *N. diardi* was universally considered conspecific with *N. nebulosa*, and so when *N. diardi* is recognised as a species it is presumably still implicitly on Appendix I. Otherwise all cats are listed on at least Appendix II, which would include *N. diardi*.

In this paper we use the MaxEnt niche distribution modelling approach, coupled with observer opinion, to make predictions regarding the current distribution of the Sunda clouded leopard on Borneo (see Kramer-Schadt et al. (2016) for details on the modelling).

RESULTS AND DISCUSSION

Species occurrence records. Of 259 occurrence records for the Sunda clouded leopard collected, 160 were from the period 2001–2011 (Table 1). Occurrence records were obtained from all political units of Borneo, with the exceptions of Brunei and South Kalimantan (Fig. 2). Of these, 40 were excluded from the analysis because of low spatial precision (over 5 km; Categories 4 and 5). Because of spatial clustering of records, and consequent search-effort bias, particularly in Sabah, many of the remaining 219 high-precision records (Categories 1–3) were omitted from analysis, leaving 48 and 94 records for the M_1 (Balanced) and M_2 (Spatial Filtering) models, respectively (see Kramer-Schadt et al., 2016).

Habitat associations. The 12 respondents to the land-cover classification questionnaire were relatively consistent in their assessment of suitable land-cover for the Sunda clouded leopard (Table 2). Forest habitats ranked most highly, and both lowland and upland forest were ranked above all other land-cover types. Lower montane forest, forest mosaics (lowland and upland) and swamp forest were considered moderately good habitat, whereas upper montane and mangrove were considered to be poor habitat, possibly suitable as movement corridors. All other non-forest habitats, and burnt forest areas, with the exception of old plantations – which were ranked as poor habitat – were considered unsuitable for the Sunda clouded leopard.

Habitat suitability index (HSI) model. These scores support the general view that the Sunda clouded leopard is a relatively adaptable species. This view is reflected in the predicted distribution shown in the habitat suitability models (Fig. 3). The models predict a widespread distribution over a large, contiguous portion of Borneo. The only exception is South Kalimantan, which is predicted to comprise largely unsuitable habitat. However, the mapped predictions of the

Table 1. Summary of the occurrence records for Sunda clouded leopard *Neofelis diardi* on Borneo.

Spatial Precision	Total No. of Records	No. of Records in M_1	No. of Records in M_2	No. of Recent Records 2001–2011
Category 1 below 500 m	161	23	53	160
Category 2 500 m – 2 km	17	6	9	11
Category 3 2–5 km	41	19	32	3
Category 4 above 5 km	18	-	-	3
Category 5 (no coordinates*)	22	-	-	0
Total	**259**	**48**	**94**	**177**

M_1 = Balanced Model; M_2 = Spatial Filtering Model (5 km); *only coarse location description was available

Table 2. Land-cover reclassification for Sunda Clouded Leopard *Neofelis diardi* based on the questionnaire results of 12 respondents working on carnivores on Borneo.

Land-cover Class	Mean of Reclassification	Range of Reclassifications
Lowland forest	3.67	3–4
Upland forest	3.11	2–4
Lower montane forest	2.22	1–3
Upper montane forest	1.11	0–3
Forest mosaics/lowland forest	2.12	*
Forest mosaics/upland forest	1.95	#
Swamp forest	2.30	1–4
Mangrove	1.44	1–3
Old plantations	1.22	0–3
Young plantations and crops	0.40	0–2
Burnt forest area	0.50	0–2
Mixed crops	0.20	0–1
Bare area	0.00	0–0
Water and fishponds	0.20	0–1
Water	0.00	0–0

*/#Calculated based on the mean of the reclassification of old plantation and *lowland forest or #upland forest, respectively.
Habitat suitability rank ranges from 0 (unsuitable) to 4 (most suitable); further detail, and on land-cover classes, in Kramer-Schadt et al. (201x).

habitat suitability index model in Fig. 3 need to be interpreted with caution (see Kramer-Schadt et al. (2016) for more details). Of note, some areas, particular in South and West Kalimantan, had little information, reflecting the lower survey efforts in these areas. Although search-effort bias has been minimised during the modelling, these areas might still be underrepresented in the distribution map especially if they are climatically distinct from the rest of Borneo. This is particularly likely for South Kalimantan which has a more pronounced dry season (see Kramer-Schadt et al., 2016: Fig. 3A). Thus, unless there are records sufficiently spatially precise to have been used in the model, the prediction cannot accurately reflect the potential for occurrence in that region. In general, further surveys are needed to verify if the lower predictions are because of the minimal survey efforts or reflect a genuine lower suitability of these areas for the species, perhaps because of different climatic conditions or because large areas have been transformed to unsuitable land-cover (see Kramer-Schadt et al., 2016: Fig. 3B).

The predicted distribution follows closely the current distribution of forest on Borneo. Notably, the species is predicted to be absent from extensive areas of plantation, particularly in much of the coastal lowlands. The predicted range encompasses a large proportion of the existing and proposed protected area network on Borneo. In Sabah, the protected areas of Tabin Wildlife Reserve and the Tawau Hills National Park and contiguous forests are predicted to be highly suitable, yet are absent from the IUCN Red List distribution map. Based on the current predicted distribution

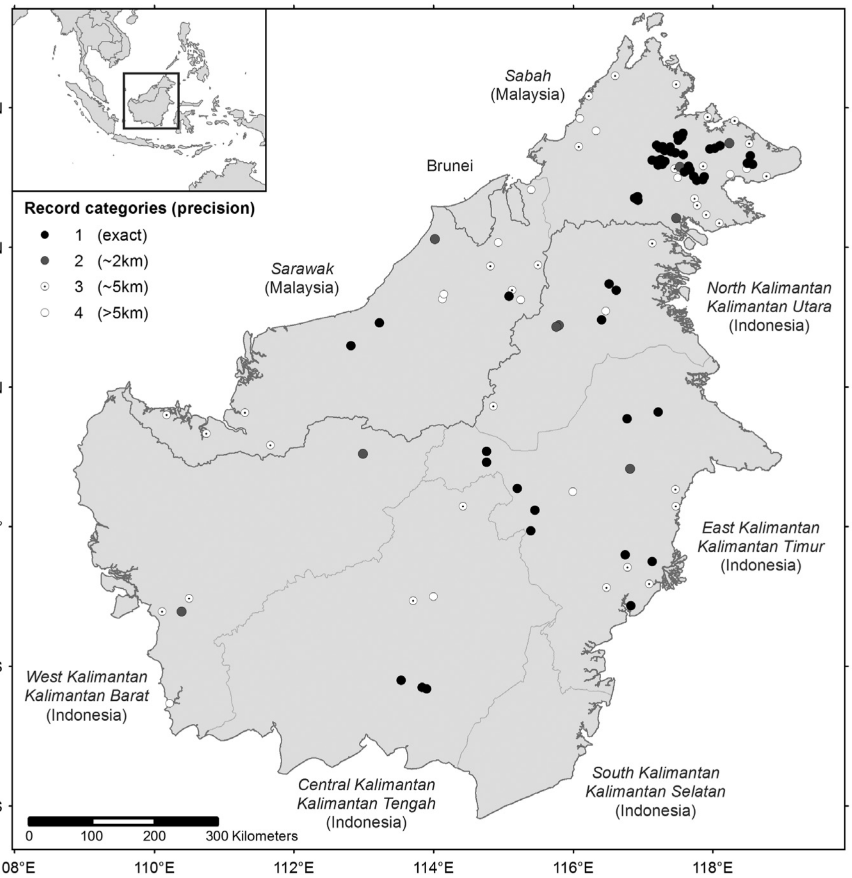

Fig. 2. Location of Sunda clouded leopard *Neofelis diardi* occurrence records on Borneo with categories of spatial precision as well as countries and state boundaries.

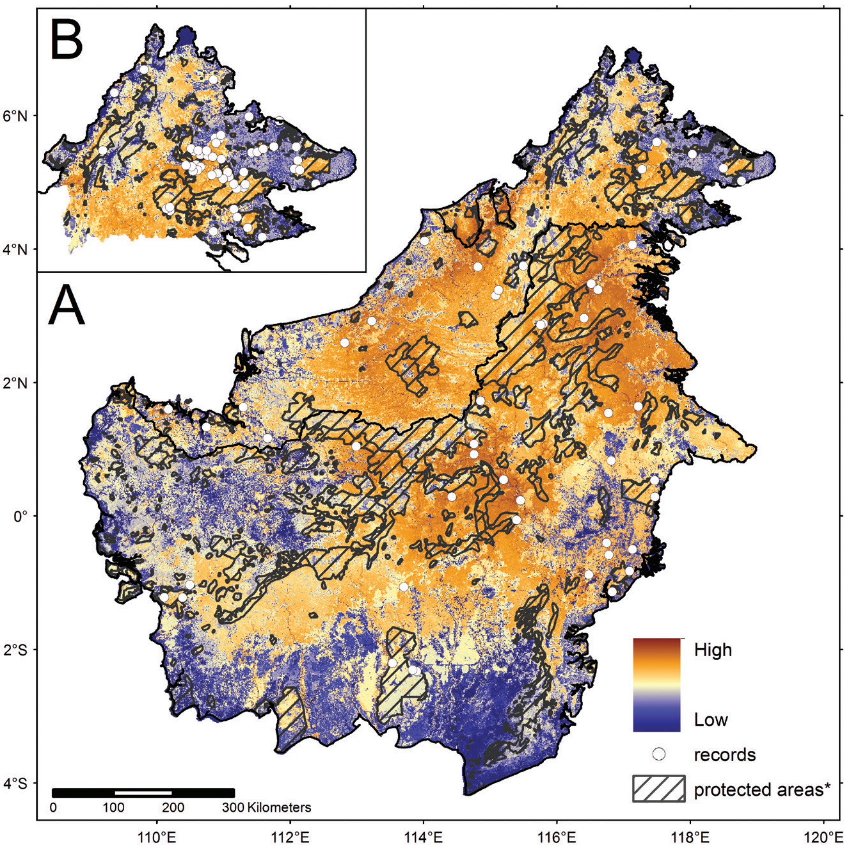

Fig. 3. Predictive Habitat Suitability Index (HSI) models for Sunda clouded leopard *Neofelis diardi* including location records used in models. A, Balanced Model for the island of Borneo; B, Spatial Filtering Model for Sabah, Malaysia. Sources for protected area information: see Kramer-Schadt et al. (2016).

the following protected areas and regions are highlighted as priorities for the conservation of the Sunda clouded leopard on Borneo:

Brunei Darussalam. Although no records were obtained from Brunei, a large proportion of it is predicted to be of high to moderate suitability for the Sunda clouded leopard, in line with the significant proportion of forest cover within the Sultanate. Although rather restricted in size with regard to the Sunda clouded leopard's plausibly extensive spatial requirements, both the Merimbun Heritage Park and Sungai Ingei Protection Forest are predicted to be highly suitable habitat. The Ulu Temburong National Park is predicted to contain areas of high and moderate suitability, and is thus also a key area for the protection of this species in Brunei.

Sarawak, Malaysia. A very large, contiguous region of the Malaysian state of Sarawak is predicted to be of high to moderate suitability for the Sunda clouded leopard. A large portion of the western third of the state and much of the coastal region (up to 75 km from the coastline) comprises settlements and large-scale oil palm plantations and contains relatively little natural forest cover; this is reflected in these regions' predicted low suitability. A number of protected areas in Sarawak are predicted to be of optimal habitat suitability, and thus of particular importance to the conservation of the Sunda clouded leopard. Such areas include the proposed Hose Mountains National Park and Batu Laga Wildlife Sanctuary, the Usan Apau National Park and the Lanjak-Entimau Wildlife Sanctuary and Batang Ai National Park. Gunung Buda National Park and the northern portion of Mulu National Park were also predicted to be of high suitability, and are thus important areas for the conservation of the Sunda clouded leopard in Sarawak. In addition, both parks are an important component in maintaining connectivity between two otherwise disjointed protected areas in Brunei, the Sungai Ingei Protection Forest and the Ulu Temburong National Park. A corridor of forest linking Ulu Temburong to Gunung Buda was also predicted to be of high suitability to the Sunda clouded leopard; this forest is currently unprotected. Forest protection is also needed to ensure connectivity between the Hose mountains, Betung Kerihun, and Kayan Mentarang, and between Mulu / Ulu Temburong and Pulong Tau / Kayan Mentarang.

Sabah, Malaysia. Much of the extensive Permanent Forest Reserve system, which includes the approximately 1 million ha Yayasan Sabah Forest Management Area (YSFMA; Reynolds et al., 2011) is predicted to be moderately to highly suitable for the Sunda clouded leopard. All protected areas in Sabah are predicted as of either moderate or high suitability, but are relatively small (the largest being the Crocker Range Park, at 139,919 ha), although largely contiguous with one another via the Permanent Forest Reserve system. The Tawau Hills Park and adjacent Ulu Kalumpang Protection Forest Reserve is an area of high predicted suitability for the Sunda Clouded Leopard in Sabah, as is the Tabin Wildlife Reserve. Both areas are threatened to some degree with isolation. For the Tawau Hills area, connectivity to the YSFMA is currently facilitated by an extensive area of timber plantations, predicted to be moderately suitable habitat. A large area of coastal mangrove forest, including the Kulamba Wildlife Reserve, although predicted to be of low to moderate suitability for the Sunda clouded leopard, potentially provides connectivity between the Tabin Wildlife Reserve and the Kinabatangan Wildlife Sanctuary, itself an area of moderate to high suitability. It is essential that efforts are made to ensure that these potentially important areas for the conservation of the Sunda clouded leopard in Sabah retain their connectivity with other areas of Sunda clouded leopard habitat.

North Kalimantan and East Kalimantan, Indonesia. A large area of North and East Kalimantan is predicted to be suitable habitat for the Sunda clouded leopard, and the provinces have perhaps the largest contiguous region of predicted high-suitability habitat for this species in Borneo. A number of protected areas lie within this zone, many of which are larger the average for Borneo. Of particular note is the Kayan Mentarang National Park (KMNP), which at 1,360,500 ha is the largest protected area on Borneo, and is predicted largely to comprise suitable habitat. East of KMNP is an extensive area of largely community and production forest that is predicted to have some of the most suitable habitat for the Sunda clouded leopard on the whole island.

South Kalimantan, Indonesia. We received no records of Sunda clouded leopard from South Kalimantan. Whether this represents an absence of this species from this province or simply a lack of survey effort is unclear (see above). Almost all South Kalimantan was predicted to be of low suitability, although the northern reaches of the Meratus mountain chain, which contain the proposed Meratus Hulu Barabai Nature Reserve, were predicted to contain moderately suitable habitat. Survey effort should focus on South Kalimantan to investigate whether the Sunda clouded leopard inhabits the province.

Central Kalimantan, Indonesia. Much of southern Central Kalimantan was predicted to be of low suitability for the Sunda clouded leopard, reflecting the extensive forest conversion in this province. The exceptions are the extensive peat swamps, lowland and heath forests of the Sabangau and Tanjung Puting National Parks, which were predicted to be moderately suitable habitat. Much of the centre and north of this province were also predicted to be suitable habitat. The forested areas of the Schwaner Range ranked quite highly and thus the protected areas of the Bukit Baka–Bukit Raya National Park, and, in particular, the sizeable Bukit Batikap I, II and III and Bukit Sepat Haung Nature Reserves, are important areas for the protection of this species in Central Kalimantan.

West Kalimantan, Indonesia. Much of West Kalimantan was predicted to be of moderate to low suitability for the Sunda clouded leopard. One of the areas predicted to be of highest suitability within the province was the Schwaner range, which lies along the border with Central Kalimantan, much of which was predicted as moderate suitability. This mountainous area encompasses the Bukit Ronga and Bukit

Perai Protection forests, and the Bukit Baka–Bukit Raya National Park. The region to the far east of West Kalimantan, bordering both Sarawak to the north and Central Kalimantan to the south, was predicted to be moderately to highly suitable. It contains both the Bukit Batutenobang Protection Forest and Betung Kerihun National Park. In addition to their prediction as among the most suitable areas for the species in West Kalimantan, these protected areas might also serve as essential connections for habitat in Central Kalimantan with that in Sarawak, and thus form perhaps the highest priority for conservation of this species in the province.

CONCLUDING REMARKS AND CONSERVATION PRIORITIES

This research adds to the growing body of knowledge regarding the distribution of the Sunda clouded leopard on Borneo. It supports the general notion that the Sunda clouded leopard might be an adaptable species and predicts that such a considerable area of Borneo is suitable that it is likely to occur in most protected areas across the island. However, a number of recent camera-trap surveys on Borneo, specifically undertaken to detect and estimate the density of the Sunda clouded leopard, failed to find the species, including in the Kabili–Sepilok Forest Reserve, Sabah (AJ Hearn, J Ross and DW Macdonald, unpublished data) and at several forest sites in Kalimantan (Cheyne et al., in prep.). Such surveys suggest that the species's presence across forested Borneo might be somewhat complex and patchier than is predicted in the current model. The differential prevalence of hunting and poaching across the island and their consequent impact on Sunda clouded leopard and prey populations, neither of which were included as covariates in the model, are likely to have a significant influence on the species's current distribution and might be partly responsible for its local extirpation from certain areas. While legislation pertaining to hunting is in place across the range states, shortages of trained staff and funds mean that local law enforcement is often unable adequately to control this threat; as a result the detrimental consequences of hunting and poaching appear to apply equally to protected and unprotected areas alike. The only single factor offering any effective protection for wildlife appears to be difficulty of access (Bennett et al., 2000). Thus, this model of the current distribution of the Sunda clouded leopard in Borneo, while providing a sound basis upon which to test hypotheses about its distribution, should nevertheless be viewed cautiously.

Mounting evidence shows that the Sunda clouded leopard is found at relatively low population densities, even in well-protected, undisturbed forests, with typical estimates of fewer than two individuals per 100 km^2 (Brodie & Giordano, 2012; Wilting et al., 2012; Cheyne et al., 2013; AJ Hearn, J Ross and DW Macdonald, unpublished data; B Loken et al., unpublished data). The differential hunting pressure across the island makes it conceivable and perhaps prudent from a precautionary standpoint, to assume that the mean, range-wide density of the Sunda clouded leopard lies below this. At present, the area of forest likely to be needed to support, long term, a viable population of Sunda clouded leopard cannot yet be determined; in excess of 3000 km^2 might be required. Thus, as Borneo's forests become ever more reduced in size and increasingly fragmented a critical conservation priority for the species will be to maintain and re-establish connectivity, for example via habitat corridors, between Sunda clouded leopard populations, particularly those residing within core protected areas. In view of this, some areas of forest predicted as being suitable habitat-types for the Sunda clouded leopard might indeed be too small and/or isolated from a viable population to hold the species indefinitely. This serves, once again, to underscore the fact that the model might be rather optimistic so should be viewed with appropriate caution.

The overall paucity of location records for the Sunda clouded leopard, particularly in the provinces of Central and West Kalimantan, Indonesia, and in Brunei Darussalam, means that efforts should thus be made to address this knowledge gap. Another focus should be to determine whether the Sunda clouded leopard is indeed absent from South Kalimantan, Indonesia. More specifically, further studies into the species's habitat associations and movement ecology, and particularly the factors that influence dispersal, are urgently needed to improve understanding of its distribution on Borneo and to facilitate the development and implementation of appropriate, spatially explicit conservation management plans. Lastly, while the *N. nebulosa* is currently listed under CITES Appendix I, which bans international trade, the Sunda clouded leopard *N. diardi* warrants also full listing under CITES Appendix I.

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