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Endangered leopards: Range collapse of the Indochinese leopard (*Panthera pardus delacouri*) in Southeast Asia

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ABSTRACT

The Indochinese leopard (*Panthera pardus delacouri*) is a genetically distinct subspecies that historically occurred throughout mainland Southeast Asia, but might have experienced recent declines in numbers and distribution. This study aimed to determine the current distribution of the Indochinese leopard, and estimate its population size, by reviewing data from camera trap and other wildlife surveys conducted during the past 20 years. Our results showed the Indochinese leopard likely now occurs only in 6.2% of its historical range, with only 2.4% of its distribution in areas of confirmed leopard presence. The leopard is extirpated in Singapore, likely extirpated in Laos and Vietnam, nearly extirpated in Cambodia and China, and has greatly reduced distributions in Malaysia, Myanmar, and Thailand. There are plausibly only two major strongholds remaining, which we consider priority sites: Peninsular Malaysia, and the Northern Tenasserim Forest Complex. We also identified a small isolated population in eastern Cambodia as a third priority site, because of its uniqueness and high conservation value. We estimate a total remaining population of 973–2503 individuals, with only 409–1051 breeding adults. Increased poaching for the illegal wildlife trade likely is the main factor causing the decline of the Indochinese leopard. Other potential contributing factors include prey declines, habitat destruction, and possibly disease. We recommend a separate IUCN assessment for the Indochinese leopard, and that this subspecies be classified as Endangered. Our findings provide important information that can help guide where conservation actions would be most effective in preventing the extinction of this subspecies.

1. Introduction

The leopard (*Panthera pardus*) has the widest distribution of any felid species, and it historically occurred throughout Africa (except Saharan desert), and in Asia from the Middle East to the Pacific Ocean (Stein and Hayssen, 2013). Its wide distribution reflects its ability to inhabit diverse habitats and consume a wide range of prey (Stein and Hayssen, 2013). Despite its adaptability, it has experienced severe declines in distribution and numbers, primarily because of habitat loss, prey declines, conflict with humans, and poaching for the wildlife trade, with the relative importance of these factors varying among regions (Henschel et al., 2008). Consequently, the leopard now occurs in mostly small and fragmented populations, especially in Asia where 5 of 8 subspecies are listed as Endangered or Critically Endangered (Henschel et al., 2008). A recent review recommended the north Chinese leopard (*Panthera pardus japonensis*) be listed as Critically Endangered because of the high risk of extinction (Laguardia et al., 2016), leaving only two subspecies in Asia with presumably high and stable

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numbers: the Indian leopard (*Panthera pardus fusca*) and Indochinese leopard (*Panthera pardus delacouri*).

The Indochinese leopard is a genetically distinct subspecies (Miththapala et al., 1996; Uphyrkina et al., 2001; Sugimoto et al., 2014) that historically occurred throughout all mainland Southeast Asian countries and southeastern China (hereafter Southeast Asia). The exact historical geographical boundary of this subspecies is not clear, and for the purposes of this paper we presume it occurred from the India-Myanmar border to Vietnam, and from Singapore to southeastern China (Miththapala et al., 1996; Uphyrkina et al., 2001), as far north as the Pearl River (Laguardia et al., 2016). As of 2008, the Indochinese leopard reportedly was still extant throughout most of the region (Henschel et al., 2008). However, recent camera trap studies suggested numbers and distribution of this subspecies might have declined, similar to that reported for other species in the region. Recent deforestation rates in Southeast Asia, the highest in the world, have coincided with a recent explosion in the illegal wildlife trade fuelled by increased demand, causing serious declines in many species (Duckworth et al., 2012; Lynam, 2010), which also could have negatively impacted the leopard. Therefore, we reviewed camera trapping and other wildlife surveys to determine the current distribution and population size of the Indochinese leopard in Southeast Asia, and propose recommendations for the conservation of this subspecies.

2. Materials and methods

2.1. Distribution

We conducted a literature search on Google Scholar and Web of Science for publications during the last 20 years (1995–2015) on the leopard in Southeast Asia, using the search terms "*Panthera pardus*" and each country of Southeast Asia. In Laos, we also included surveys from the early 1990s, because numerous initial wildlife surveys occurred during this period just after the country was opened to foreign researchers. Because this database might not have included all documents, we also searched gray literature, especially those by local organizations operating in Southeast Asia that might have conducted wildlife surveys. When necessary, we contacted the authors for additional information. In addition, we directly contacted organizations that conducted wildlife surveys in Southeast Asia seeking unpublished data on presence/absence of leopard. Most data used in our review came from camera-trap surveys conducted within protected areas (PAs), thus notional presence or absence could be determined. Other data came from wildlife sign surveys, including direct sightings, tracks, and scats. We used all records to produce an updated map of the distribution of the Indochinese leopard. Areas were considered "confirmed" if leopard was detected in wildlife surveys from 2000 to 2015, whereas areas were considered "potential" if leopard records were from 1995 to 1999. An exception was Myanmar, where we considered "potential" records from 1995 to 2001, given that only older records were available, and these might not represent the current distribution of leopard due to increases in poaching during the last decade. Also in Myanmar, several PAs listed leopard on their fauna lists (Instituto Oikos and BANCA, 2011) but without confirmed records, so these were classified as potential, unless camera trapping surveys failed to detect leopard there. For all countries, we also considered areas "potential" if satellite imagery showed forests contiguous with confirmed sites, especially those between different confirmed areas. Although the leopard is a habitat generalist, due to poaching this species is now primarily restricted to forest patches in Southeast Asia. Areas were classified as "absent" if camera trapping surveys with ≥500 trap days or other extensive wildlife surveys failed to detect leopard. Also, if leopard was initially detected at a site, but subsequent surveys failed to detect it, then we assumed leopard had become extirpated and we considered these areas as "absent". Because leopard, especially in small populations, might have been present in some areas but was not detected in surveys for various reasons (e.g., short length of study, small area covered), we also used expert opinion with local knowledge to confirm if our results adequately reflected the current status of leopard in the area.

2.2. Population estimate

To calculate total population size for each country, we multiplied the area of distribution (confirmed and potential) by an inferred density range. The density ranges were based on results from wildlife surveys and levels of enforcement of each country. We assumed 60% occupancy for all sites with confirmed and potential distribution because leopard does not occupy sites uniformly when factors such as tiger densities, prey densities, habitat, and human disturbance are considered (Carter et al., 2015; Steinmetz et al., 2013). We chose 60% occupancy because previous camera trap studies in Asia showed leopard had occupancy ranging between 31 and 62% (Carter et al., 2015; Steinmetz et al., 2013; S. Rostro-García and WWF Cambodia, unpubl. data), thus using the approximate upper value would help ensure that leopard numbers were not underestimated.

For Cambodia, China, and Myanmar, we assumed a low density range of 0.5–1.5 leopard/100 km^2, based on similarly high levels of poaching and low levels of effective enforcement across the countries, and considering a study in Cambodia that estimated a density of about 1 leopard/100 km^2 in 2014 (S. Rostro-García and WWF Cambodia, unpubl. data). For Malaysia, we assumed a medium density range of 1.0–3.0 leopard/100 km^2, based on relatively higher levels of effective enforcement and a recent study which estimated a density of 3.0 leopard/100 km^2 (Hedges et al., 2015). We assumed this was the maximum density for leopard in the country, because this population lived under optimal conditions (e.g., low tiger numbers, high prey numbers, suitable habitat). We chose a density of 1.0 leopard/100 km^2 as the minimum, assuming other areas were less optimal for leopard, similar to the density reported in Cambodia. In Thailand, we assumed a high density range of 2.5–5.0 leopard/100 km^2, given relatively higher levels of effective enforcement (Duangchantrasiri et al., 2016) and that previous leopard densities from several PAs were within that range (Simcharoen and Duangchantrasiri, 2008; Steinmetz et al., 2009). Because PAs in Thailand are part of large PA complexes, we used the total area of the complexes, either as confirmed or potential, if leopard was detected in at least one PA within them. However, a PA was excluded from the total area of a complex if surveys failed to detect leopard in that particular PA. Another exception was the Hala-Bala Complex, because leopard was detected only in one PA within the complex (Hala Bala Wildlife Sanctuary [WS]), thus only the size of that PA was used in the calculation.

The total population size (N) includes adults and subadults that are not part of the breeding population and which might never produce offspring. Therefore, we also estimated effective population size (N_e), an estimate of the genetic size of the population, which determines the number of reproductively viable mature individuals that contribute offspring which themselves reproduce (hereafter breeding adults). We estimated N_e for the remaining Indochinese leopard populations using a N_e:N ratio of 0.42, which was used previously for leopard in Africa (Spong et al., 2000). Although this ratio might not be appropriate for all leopard populations in Southeast Asia, we assumed it to be similar to that of leopard from Africa given that data on N_e were not available for leopard in Asia. Also, the estimation of N_e can later help with the IUCN assessment of this subspecies, as estimation of total mature individuals is needed to help determine classification. Finally, to evaluate the sensitivity of our estimated results, we calculated N and Ne using extreme values of leopard occupancy (10% and 90%).

3. Results

We reviewed 146 wildlife surveys from 109 sites from 6 countries within the historic range of the Indochinese leopard (Appendix A), in addition to using previous reviews for southeastern China (Laguardia et al., 2016) and Singapore (Corlett, 1992). The Indochinese leopard

now likely occurs only in 6.2% of its historical range, with only 2.4% of its distribution in areas of confirmed leopard presence. Our estimated leopard distribution is 91% smaller than that estimated by the IUCN in 2008 for Southeast Asia (Henschel et al., 2008), although the latter was likely an overestimation of the leopard distribution in the region due to lack of information. The current distribution of the Indochinese leopard is restricted to several small and highly fragmented subpopulations (Fig. 1). The total estimated area of confirmed (63,236 km^2) and potential (103,089 km^2) distribution in Southeast Asia is 166,325 km^2, with an estimated remaining population of 973–2503 total individuals (N), with 409–1051 breeding adults (N_e). Our sensitivity analysis using 10% and 90% occupancy showed that N ranged from 162 to 3755 total individuals, whereas N_e ranged from 68 to 1577 breeding adults. Below we provide a detailed review of the Indochinese leopard distribution and population size within each country of its historical range.

Cambodia: We reviewed 34 wildlife surveys from 26 sites (Appendix A). Leopard now occurs only in 8.0% of its historical range in the country, and there appears to be only one remaining viable population in the Eastern Plains Landscape (EPL). Leopard was recently detected in four PAs within EPL, as well as two small nearby areas (Appendix A; Fig. 1). In Mondulkiri Protected Forest (PF), the largest PA in the country with the highest biodiversity, the leopard density declined about 70% from 2009 (3.6 leopard/100 km^2; Gray and Prum, 2012) to 2014 (1.0 leopard/100 km^2; S. Rostro-García and WWF Cambodia, unpubl. data). Because the same camera trapping methods (field protocol and statistical analysis) were used between studies, and prey numbers were shown to be stable between periods (WWF Cambodia, unpubl. data), poaching for the wildlife trade was likely the main reason for the decline of leopard numbers. In fact, recently interviewed poachers of the EPL stated that they received $55–$60 per kg of leopard bones from Vietnamese traders (Prum S., unpubl. data). Consequently, unless more effective protection is provided, poaching might soon lead to the extirpation of the leopard population in EPL, similar to that recently observed for tiger in the same landscape (O'Kelly et al., 2012). Leopard also was recently detected in the Northern Plains Landscape (NPL), however in 3 years of extensive camera trapping in Preah Vihear PF, only 2

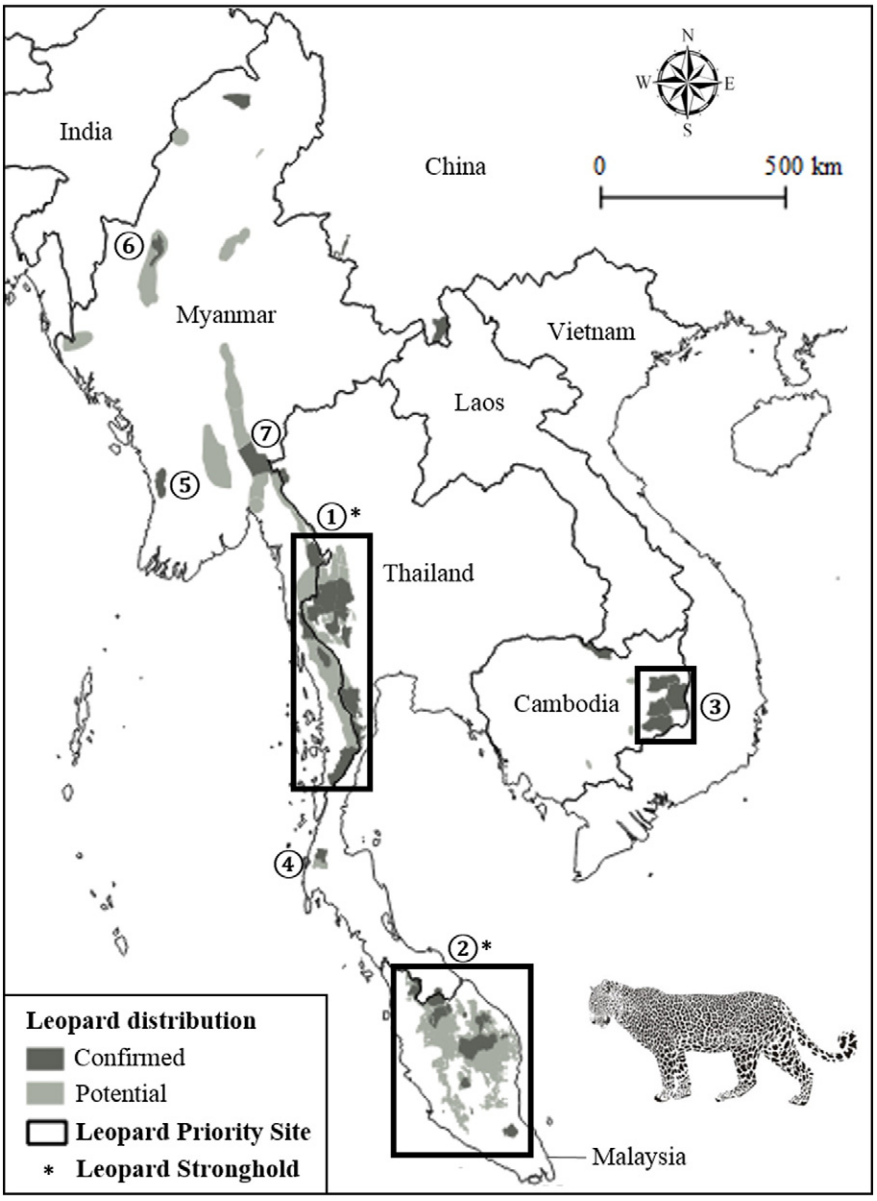

Fig. 1. The current (confirmed and potential) estimated distribution of the Indochinese leopard (*Panthera pardus delacouri*) in Southeast Asia. The areas surrounded by rectangles indicate leopard priority sites: (1) Northern Tenasserim Forest Complex; (2) Peninsular Malaysia, and; (3) Eastern Plains Landscape; whereas the asterisks indicate the two leopard strongholds. Other sites with potentially viable populations are: (4) Khlong Saeng-Khao Sok Complex; (5) Rakhine Yoma Elephant Range WS; (6) Alaungdaw Kathapa-Mahamyaing complex, and; (7) northern Karen (Kayin) State.

individuals were detected, with none detected during the final year (A. Suzuki, unpubl. data). Similarly, leopard was not detected in adjacent Kulen Promtep WS (Edwards et al., 2012) or in nearby PAs across the border in Thailand (Lynam et al., 2006; T. Redford, Freeland Foundation, pers. comm.), indicating the leopard population in this complex is very low and probably not viable. Leopard seems to have been extirpated from the Cardamom Mountains, because no individuals were detected in the region despite recent camera trapping in several of the main PAs within the complex (Appendix A). Similarly, leopard is probably now extirpated from the Northeastern Complex, despite being detected in Virachey National Park (NP) in 1999–2001, as a recent study failed to detect leopard (Appendix A). Because both the Cardamom Mountains and Northeastern complexes still contain extensive forests and apparently sufficient prey numbers (FFI Cambodia and HabitatID, unpubl. data), extirpation of leopard in these regions was likely because of poaching for the wildlife trade, as snaring is widespread in these areas. Outside of the forest complexes, leopard was not detected in 10 of 13 sites (Appendix A). Although leopard was recently detected in Kandal Province, southern Cambodia (Appendix A), we assume this population is not viable due to high levels of habitat degradation and poaching, as well as relatively high human population. All leopard records from Cambodia are of spotted individuals. The total area of confirmed and potential leopard distribution is 14,605 km^2, and the population estimate is 44–132 total individuals, with 18–55 breeding adults.

China: In southeastern China, leopard now occurs only in 0.4% of its historical range. A recent review found that the Indochinese leopard was detected by camera traps only in Nangunhe (2012–14) and Xishuangbanna (2008) PAs, both in southwestern Yunnan Province (Laguardia et al., 2016; Fig. 1). Laguardia et al. (2016) concluded that each PA contains only a few individuals and populations are unlikely to recover because of low prey numbers, and high levels of habitat loss and poaching in the region, thus the Indochinese leopard in the country probably is on the verge of extirpation. The total area of confirmed distribution in southeastern China is 2483 km^2, and the population estimate of remaining Indochinese leopard is 8–22 total individuals, with 3–9 breeding adults.

Lao PDR (Laos): We reviewed 12 wildlife surveys from 6 sites (Appendix A). Reports of leopard by local people were still somewhat widespread in Laos during the early 1990s (Duckworth et al., 1999), however these might have been unreliable because confirmed records came only from Nakai-Nam Theun National Protected Area (NPA) and Nam Ghong Provincial Protected Area (W. Duckworth, pers. comm.), indicating leopard already was likely rare in Laos by the 1990s. Recent (post-2000) surveys suitable to assess leopard status have covered only a relatively small proportion of presumably suitable habitat in the country, and recorded leopard in only one landscape, the Nam Et-Phou Louey (NEPL) NPA in northern Laos. Although this is one of the largest and arguably best protected PAs in the country (Johnson et al., 2006), leopard was last photographed in NEPL in 2004 despite extensive camera-trapping and DNA testing of >500 scats since that time (WCS Lao PDR and Panthera, unpubl. data; Appendix A). In Nakai-Nam Theun NPA in central Laos, the leopard population was estimated to be 30–40 individuals in the mid-1990s (Timmins and Evans, 1996), yet no leopard was detected there during extensive camera trapping conducted from 2006 to 2011 (Coudrat et al., 2014). Likewise, in southern Laos there are no recent records from Nam Kading, Xe Sap, and Xe Pian NPAs, despite evidence of leopard in the latter two PAs during the 1990s (Appendix A). Although rangers reported leopard sign in Nam Pouy NPA in northwestern Laos in 2015 (T. Gray, WWF Greater Mekong, pers. comm.), surveys are needed there to confirm leopard presence. Although several areas of presumably suitable habitat in Laos remain inadequately surveyed to infer status of leopard within them, leopard is unlikely to occur in a viable population within these areas, especially given that recent surveys have targeted the largest PAs in the most remote areas in the country (e.g., NEPL and Nakai-Nam Theun). Leopard seemingly has disappeared from areas that appear to contain sufficient habitat and prey (e.g., NEPL), suggesting that local extirpations were likely because of poaching for the wildlife trade, similar to that observed in Cambodia. We conclude there are no viable leopard populations remaining in Laos, and that the leopard is now likely functionally extinct, if not fully extirpated, from the country, with the bulk of the decline and range contraction probably occurring by 2000.

Malaysia (peninsular): We reviewed 29 wildlife surveys from 22 sites (Appendix A). Leopard now occurs only in 35.6% of its historical range in the country. In contrast to other countries in Southeast Asia, leopard still occurs throughout most forests in the country, including large complexes in the north (Belum-Temengor), central (Taman Negara), and south (Endau-Rompin; Fig. 1; Appendix A). Leopard also has been detected in fragmented secondary forests southwest of Kuala Lumpur (Sanei et al., 2011), and other fragmented forests throughout the country (Fig. 1; Appendix A). Peninsular Malaysia clearly is one of the remaining strongholds for the Indochinese leopard, although the population might be under threat from recent increases in poaching. For example, there is recent evidence of poaching of leopard in Peninsular Malaysia (Rais, 2013), which might cause a decline in the leopard population, similar to that recently reported for tiger in the same region (Kawanishi, 2015). In fact, outside of the 3 major complexes mentioned above, leopard was not detected in 36% (5 of 14) of surveyed sites (Appendix A). Nevertheless, we considered most forested areas outside of PAs as potential, unless leopard was not detected in an area, given that poaching is presumably not as extensive as in other countries of Southeast Asia. All records from Peninsular Malaysia are of melanistic leopard (Kawanishi et al., 2010), except for a few individuals (Tan et al., 2015). The total area of confirmed and potential distribution is 47,051 km^2, and the population estimate is 282–847 total individuals, with 119–356 breeding adults.

Myanmar: We reviewed 27 wildlife surveys from 23 sites (Appendix A). Leopard now occurs only in 11.3% of its historical range in the country. From 1999 to 2004, leopard was detected in only 9 of 18 survey areas located throughout the country (Zaw et al., 2014), and distributions likely decreased since that time because of increased poaching, similar to that reported for tiger in Myanmar (Lynam, 2010). For example, although the Northern Forest Complex has several large PAs, leopard is probably functionally extinct there. In this complex, the only recent verified leopard records were from the core zone in Hukaung Valley WS in 2007, despite annual camera trapping throughout the entire PA from 2001 to 2011 (Naing et al., 2015), as well as camera trapping in several other PAs in the complex (Zaw et al., 2014; Appendix A). Similarly, in Chatthin WS, a steady decline in leopard was reported until they were on the verge of extirpation in the late 1990s (Aung et al., 2004). Leopard records since 2005 are rare, and include only one complex and three small areas with potentially viable populations (Fig. 1, Appendix A). The Southern Forest Complex presumably contains the largest viable population of leopard in the country (Fig. 1; Appendix A). This complex is contiguous with two large complexes in Thailand, which together comprise the Northern Tenasserim Forest Complex. Outside of this complex, the three small areas with potentially viable populations are Alaungdaw Kathapa–Mahamyaing Complex, Rakhine Yoma Elephant Range WS, and northern Karen (Kayin) State (Fig. 1). Our conclusion is based on recent leopard records, size of area protected, prey availability, habitat quality, levels of human disturbance, and levels of effective enforcement. Leopard records from Myanmar include both spotted and melanistic individuals. The total area of confirmed and potential distribution is 74,440 km^2, and the population estimate is 223–670 total individuals, with 94–281 breeding adults.

Singapore: Historically leopard occurred in Singapore, but was extirpated from the island state as it became developed during the past century (Corlett, 1992).

Thailand: We reviewed 30 wildlife surveys from 20 sites (Appendix A). Leopard now occurs only in 5.4% of its historical range in the country. Currently, leopard occurs only in 4 of 19 PA complexes located in the

country: Western Forest Complex (WEFCOM), Kaeng Krachan-Kuibiri Complex, Khlong Saeng-Khao Sok Complex, and Hala-Bala Complex. In late 1990s and early 2000s, there were a few leopard records in forest complexes in the north-central (Phu Khieo-Nam Nao Complex; Borries and Koenig, 2014) and south-central parts of Thailand (Dong Phayayen-Khao Yai Complex; Lynam et al., 2006; Ngoprasert et al., 2012), but extensive camera trap surveys have indicated they are now likely extirpated from these areas (Appendix A). In northern Thailand there have been few wildlife surveys, but viable populations of leopard are unlikely to occur there given high rates of deforestation and poaching. Although leopard was recently recorded in Salawin NP (Appendix A) in northwestern Thailand, this site is on the border near a confirmed population in Myanmar, and thus we do not consider it a viable population within Thailand. The WEFCOM is the largest complex where leopard still occurs, and within this complex Huai Kha Khaeng WS is the best protected PA (Duangchantrasiri et al., 2016) and probably has the highest leopard density (Rabinowitz, 1989; Simcharoen and Duangchantrasiri, 2008). Nevertheless, leopard was not detected in all PAs within the complex (Appendix A), and its population in Huai Kha Khaeng WS declined 38% over 3 years during the late 1990s (Simcharoen and Duangchantrasiri, 2008), indicating this leopard population might be under threat. Within the Kaeng Krachan-Kuibiri Complex, Kuiburi NP was reported to have relatively high leopard densities (Steinmetz et al., 2009). This complex and WEFCOM, together with the adjacent Southern Forest Complex in Myanmar, comprise the Northern Tenasserim Forest Complex. Outside of these complexes, leopard was recently detected only in the peninsula, including both the Khlong Saeng-Khao Sok Complex and Hala Bala WS (Appendix A). The leopard population in Hala Bala WS is continuous with that in Malaysia, thus is not an isolated population. In contrast, the Khlong Saeng-Khao Sok Complex appears to be isolated, and we assume this population to be relatively small because only two photographs were obtained in Khlong Saeng WS in 2014 despite extensive camera trapping (Appendix A). All leopard records from Hala Bala and Khlong Saeng-Khao Sok Complex are from melanistic individuals, whereas records from other areas in Thailand include both spotted and melanistic individuals. The total area of confirmed and potential distribution is 27,747 km^2, and the population estimate is 416–832 total individuals, with 175–350 breeding adults.

Vietnam: We reviewed 14 wildlife surveys from 12 sites (Appendix A). Recent records of leopard from Vietnam are rare. From 1995 to 2013, there were no photographs of leopard from camera-trapping studies in the country, including those in the largest and best protected PAs (Appendix A). The last unverified report of leopard from Vietnam was probably from the early 2000s in Yok Don NP, in central Vietnam (Eames et al., 2004), which might have been transient leopard originating from the adjacent population in eastern Cambodia. It is doubtful that leopard still occurs there given high levels of hunting and snaring in Vietnam, which have decimated populations of smaller felids in the country (Willcox et al., 2014). We conclude there are no viable leopard populations in Vietnam, and that this species is likely extirpated from the country.

4. Discussion

The Indochinese leopard now likely occurs only in 6.2% of its historical range in Southeast Asia. This subspecies is extirpated in Singapore, likely extirpated in Laos and Vietnam, nearly extirpated in Cambodia and China, and has a greatly reduced distribution in Malaysia, Myanmar and Thailand (Fig. 1). This dramatic decline is exceptional, given the relatively high adaptability of this species. However, this range collapse is similar to that recently reported for tiger in Southeast Asia (Lynam, 2010), suggesting that poaching for the wildlife trade is probably the greatest factor contributing to the decline of leopard in the region. Although tiger parts are worth more than leopard parts, the latter often are used as substitutes for tiger parts given their higher availability (Raza et al., 2012), thereby causing increased demand and higher prices for leopard parts, especially when tiger numbers decrease. The relatively high price paid for leopard bones by Vietnamese traders in Cambodia suggests high demand for leopard parts in Vietnam. A rising trend of poaching leopard for the wildlife trade in China has been reported from India (Raza et al., 2012; Mondol et al., 2015) and Myanmar (Nijman and Shepherd, 2015), indicating that demand from China also is driving heavy poaching of leopard in South and Southeast Asia. More information is needed about the demand for and destination of leopard parts in Southeast Asia, so that governments can plan more efficient law enforcement operations and non-governmental organizations (NGOs) can initiate effective campaigns orientated towards reducing demand. In general, the lack of effective enforcement in PAs across Southeast Asia, along with cultural differences, may explain why leopard populations have disappeared faster in this region compared to populations in the Indian subcontinent.

Other potential factors contributing to the range collapse of leopard in Southeast Asia include prey depletion, habitat destruction, and possibly disease. Throughout Southeast Asia, populations of non-human primates and large (>5 kg) ungulates, typical prey of leopard in the region (Grassman, 1999; Rabinowitz, 1989), are well below carrying capacity because of overhunting by humans, even within PAs (Johnson et al., 2006; Kawanishi et al., 2013; Naing et al., 2015; Steinmetz et al., 2010). Such low numbers of primary prey are likely to hinder leopard recovery in the region. Therefore, conservation actions to recover leopard populations in Southeast Asia also should include the conservation and recovery of their main prey species.

Habitat loss and fragmentation also are threats to the leopard in Southeast Asia, primarily because these are closely associated with high levels of human hunting. The deforestation rate in Southeast Asia is the highest of all tropical regions, with much of it inside PAs (Heino et al., 2015), and the rate is still increasing (Miettinen et al., 2011; Sodhi et al., 2010). For example, Malaysia and Cambodia now have among the highest rates of forest loss in the world (Hansen et al., 2013). One of the precursors of deforestation in the region is road development, which alone has been shown to increase hunting pressure on mammals (Clements et al., 2014). From 2000 to 2010, the area of primary or secondary forests combined decreased in all Southeast Asian countries, most of which was because of conversion to oil palm and rubber plantations, as the price of these commodities increased 130% and 333%, respectively, during the same period (Wilcove et al., 2013). Because <10% of Southeast Asian forests are under some form of protection, and prices of luxury wood, palm oil, and rubber are expected to increase, habitat loss in the region is expected to continue (Sodhi et al., 2010) and thus is likely to have increasingly negative impacts on leopard populations.

Disease, especially canine distemper virus (CDV), might be another factor negatively affecting leopard populations in Southeast Asia. Although not originally thought to be common in felid species, CDV outbreaks have increasingly been shown to devastate *Panthera* populations during the past 20 years. For example, in the Serengeti, an outbreak of CDV in the mid-1990s caused a 30% decline of the lion (*Panthera leo*) population, along with deaths of an unknown number of leopard (Roelke-Parker et al., 1996). The CDV was recently reported in Amur leopards (*Panthera pardus orientalis*; Wildlife Conservation Society Russia Program, 2015), and outbreaks of this disease recently caused a 36% decline in a population of Amur tiger (*Panthera tigris altaica*; Gilbert et al., 2015). In addition, CDV also has caused tiger deaths in India and possibly Sumatra (Gilbert et al., 2015; ProMED, 2013), suggesting it can occur in leopards in southern Asia. Although CDV may not affect large leopard populations, it likely can increase extinction rates in small isolated populations, similar to that shown for tigers (Gilbert et al., 2014). Importantly, CDV outbreaks in *Panthera* populations typically originate in local village dogs (Roelke-Parker et al., 1996). Consequently, leopard might be more susceptible to CDV than tiger, because the leopard tends to range more near human dwellings (Athreya et al., 2013;

Odden et al., 2010) and prey on dogs more often (Butler et al., 2014) than do the tiger. However, more information is needed on the prevalence of CDV in leopard, and the potential impact this disease might have on leopard populations. We recommend that conservation actions for leopard in Southeast Asia include the prohibition of dogs from PAs, to prevent the transmission of CDV and other lethal diseases to the remaining leopard populations.

Our results showed there are plausibly only two remaining strongholds for the Indochinese leopard, Peninsular Malaysia and the Northern Tenasserim Forest Complex, and we consider these high priority sites. Leopard populations in both strongholds appear to be fragmented and under threat from poaching, and thus might be in decline. Pending the unlikely discovery of other such populations, we recommend that conservation actions should be directed to protecting these two critical source sites for the Indochinese leopard, comparable to strategies proposed for conserving the remaining tiger populations (Lynam, 2010; Walston et al., 2010). The Northern Tenasserim Forest Complex is not managed as a whole, and there is no international cooperation in planning and management between Myanmar and Thailand. Several PAs on Thai side of the border receive significant national and international funding for conservation, enforcement, and community engagement activities, which has resulted in the sustained decrease in poaching in at least two PAs (Duangchantrasiri et al., 2016; Steinmetz et al., 2014). In contrast, PAs on the Myanmar side of the border receive almost no funding. Therefore, we recommend greater investment in conservation and enforcement for PAs throughout the Northern Tenasserim Forest Complex, especially on the Myanmar side of the border, and that international efforts be made to manage this complex as a single unit. Alarmingly, the Dawei Special Economic Zone is planning to build a major road between Dawei, Myanmar, and Bangkok, Thailand, which would bisect the Northern Tenasserim Forest Complex on both sides of the border (Helsingen et al., 2015). The proposed road would further fragment this important forest complex, potentially harming populations of leopard and other wildlife (Helsingen et al., 2015). Such a major economic development proposed within one of the last strongholds of the Indochinese leopard, reinforces the need for more conservation investment and better management of this forest complex.

In both priority sites, the considerable effort made by several NGOs and government bodies to monitor and conserve tiger populations, especially in core areas of PAs, presumably would benefit leopard. However, additional leopard-specific conservation actions might be necessary in these priority sites, to enhance leopard populations outside of core zones or in other areas where tiger conservation actions are absent. For example, if tiger recovery in core zones is successful, such efforts might not necessarily be beneficial to leopard, because of the antagonistic interactions between the two species. Tiger sometimes kill and spatially displace leopard, thus leopard avoid optimal habitat where there is high risk of encountering tiger (McDougal, 1988; Odden et al., 2010; Seidensticker, 1976; Steinmetz et al., 2013). Consequently, tiger recovery might result in lower numbers of leopard, even in well protected PAs (Harihar et al., 2011; Mondal et al., 2012). The exclusion of leopard by tiger in core zones might result in increased numbers of leopard in buffer zones or unprotected areas, thereby resulting in greater rates of human-leopard conflict, particularly livestock predation (Harihar et al., 2011; Odden et al., 2010). Increases in human-leopard conflict in buffer zones or unprotected areas often results in retaliatory killings by humans (Chaudhari et al., 2013; Kala and Kothari, 2013), which, together with poaching for the wildlife trade, can lead to sink populations outside of PAs (Jutzeler et al., 2010). In fact, the exclusion of leopard by tiger in core areas, together with higher leopard mortality by humans in buffer zones and unprotected areas, might explain why leopard was extirpated before tiger in certain regions of Southeast Asia, including Laos (e.g., NEPL) and central Thailand (e.g., Phu Khieo- Nam Nao and Dong Phayayen-Khao Yai complexes; Ngoprasert et al., 2012). That said, high numbers and diversity of prey likely helps to facilitate coexistence between tiger and leopard, via selection for different sized prey classes (Karanth and Sunquist, 1995) and mutual consumption of abundant prey (Lovari et al., 2015). Therefore, recovery of prey populations to relatively high numbers might be necessary to allow the coexistence of tiger and leopard within PAs, especially in relatively small and isolated PAs where large felid competition presumably would be highest.

Even if poaching is suppressed within PAs, fragmentation of leopard populations among small isolated reserves could remain a problem (Jutzeler et al., 2010). To ensure the survival of a viable leopard metapopulation in the long term, the connectivity of subpopulations in Southeast Asia must be secured through establishing or maintaining corridors across the landscapes whenever possible. For example, the presumably small population in the Khlong Saeng-Khao Sok Complex is located between the two strongholds (i.e. Peninsular Malaysia and Northern Tenasserim Forest Complex), and thus might form a stepping stone, linking both critical source sites into one large metapopulation, possibly via dispersal across suboptimal habitat. However, more research is needed to confirm if this leopard population is viable, if it is genetically linked to either priority site, and if potential corridors could be established. Nevertheless, given the limited resources currently available for leopard conservation, the establishment and enforcement of corridors across the landscape should be weighed against dedicating those resources to enhancing the long-term viability of priority sites.

Outside the two large source sites, priority also should be given to conserve the small and isolated leopard population in the EPL of eastern Cambodia. Not only does the EPL contain the only remaining population of pure spotted leopard in Southeast Asia, but it also contains the last remaining population in the region inhabiting a landscape dominated by open dry deciduous forests. In addition, the tiger was recently extirpated from the EPL (O'Kelly et al., 2012; WWF Cambodia, unpubl. data), leaving the leopard as the largest remaining apex carnivore in the ecosystem. A recent study in the EPL showed that banteng (*Bos javanicus*) was one of the main prey of leopard (S. Rostro-García et al., unpubl. data), indicating this is one of the few ecosystems in the world where leopard regularly prey on an ungulate species weighing >400 kg (Hayward et al., 2006). A conservation plan for leopard in EPL must be developed and implemented, especially because its density in one of the PAs decreased ca. 70% from 2009 to 2014 (S. Rostro-García and WWF Cambodia, unpubl. data). Certain actions should be taken immediately, particularly anti-poaching efforts concentrated in core zones, to prevent the extinction of this unique subpopulation of high conservation value.

In addition to the priority sites, three small isolated populations appear to occur in Myanmar (i.e., Mahamyaing-Alaungdaw Kathapa complex, Rakhine Yoma Elephant Range WS, and northern Karen [Kayin] State), but future research is needed to confirm if these leopard populations are viable in the long-term. Future surveys might detect leopard in other areas of Southeast Asia not covered in our review, but such populations are unlikely to be viable in the long-term because of lack of effective enforcement coupled with high rates of poaching and deforestation in the region. Nevertheless, we encourage more surveys in additional areas to better document the status of leopard throughout the region.

5. Conclusion

Because of a dramatic range collapse, we recommend that the IUCN make a separate intraspecific assessment for the Indochinese leopard. Currently, the IUCN classifies *Panthera pardus* as Near Threatened (Henschel et al., 2008), which includes the Indochinese leopard. However, given that the Indochinese leopard now likely occurs only in 6.2% of its historical distribution in Southeast Asia, with only 2.4% in areas of confirmed leopard presence, and has an estimated population size of 973–2503 individuals remaining with only 409–1051 breeding adults, we recommend that the Indochinese leopard be classified as Endangered by the IUCN (criteria A2b,c,d; A3b,c,d; C1). Furthermore, our sensitivity analysis showed that even when assuming 90% occupancy of leopard in sites across its distribution, the maximum number of

breeding adults was 1577 individuals, still below the 2500 threshold for listing as endangered by the IUCN. Given that immediate threats, including poaching and deforestation, are likely to continue, such a classification is not only justified, but would bring important conservation attention to a unique subspecies that is heading towards extinction.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.07.001.

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