Ecology and conservation of Critically Endangered Leopard (*Panthera pardus*) in Southeast Asia



A thesis submitted for the degree of
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by

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Declaration

I declare that this thesis, "Ecology and conservation of Critically Endangered Leopard (*Panthera pardus*) in Southeast Asia", is my own work. Contributions by other authors to any of the manuscripts discussed are stated in section 1.7.2. None of the work submitted for this thesis has been submitted, in whole or part, for any previous degree application.

Abstract

Ecology and conservation of Critically Endangered Leopard (*Panthera pardus*) in Southeast Asia

A thesis submitted by Susana A. Rostro García *in fulfilment of the degree of Doctor of Philosophy in Zoology*
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Although widely considered the epitome of adaptability, the Leopard (*Panthera pardus*) has experienced severe declines in distribution and numbers worldwide, yet its conservation status in several regions remains unknown. This is especially true for Southeast Asia where two understudied subspecies of Leopard occur: the Indochinese (*P. pardus delacouri*) and Javan (*P. pardus melas*) Leopard. The present study was conducted to gather information on the current status and ecology of these Leopard subspecies in Southeast Asia. Chapter 2 showed that the Indochinese Leopard now likely occurs in about 2-6% of its historical range, which led to its recent uplisting as Critically Endangered by the IUCN. Using data from the largest camera-trap study ever conducted for Leopard in the region, Chapter 3 revealed that densities within key populations in Cambodia, Thailand, Malaysia, and Indonesia were among the lowest ever reported for the species, suggesting the overall prognosis of the Leopard is becoming increasingly bleak in the region. Illegal human activities, which likely were influenced by religious beliefs, socio-economic status, and geographical location, affected the densities, habitat use and activity patterns of Leopard. Using Leopard as case study, Chapter 4 investigated the performance of spatially explicit capture-recapture (SCR) models in low-density populations surveyed with camera traps, and provided recommendations to facilitate the applicability of SCR methods under similar conditions for Leopard and other low-density species. By using DNA confirmed scats, Chapter 5 corroborated the dietary adaptability of Leopard, including the unexpected predation on Banteng (*Bos javanicus*; 600-800 kg), and showed that predation by this apex carnivore only had a relatively small impact on ungulate populations in eastern Cambodia. Using a novel approach, Chapter 6 investigated the long-term population dynamics of the Indochinese Leopard in a priority site in eastern Cambodia, and found that this unique population is under imminent risk of extirpation, likely due to increases in human-caused mortalities. Chapter 7 looked at the implications of the findings of this thesis and highlighted priorities for Leopard

conservation in Southeast Asia. This thesis offers new insights and novel approaches to study Leopard using reliable and repeatable techniques, thus aiding future studies. Overall, this thesis improves the knowledge of the species in the region and provides baseline data for several globally important populations, thereby facilitating monitoring and guiding conservation efforts for Leopard in the extremely biodiversity rich but highly threatened ecosystems of Southeast Asia.

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It seems surreal to be writing the acknowledgments of a dissertation that I feel started a lifetime ago, with several unexpected twists and turns along the way, including earthquakes, a pandemic, change of project, scorpion stings, graceless falls, the loss of a homeland and the passing of several dear people along the way. If one thing is clear in the end, is that none of this would have been possible without the support of many, which with their gestures, great or small, made this long journey an achievable one.

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List of Acronyms

AIC	Akaike's Information Criterion
BCI	Bayesian Credible Intervals
CDV	Canine Distemper Virus
DTC	Dungun Timber Complex
EPL	Eastern Plains Landscape
HKK	Huai Kha Khaeng Wildlife Sanctuary
HPDI	Highest Posterior Density Intervals
IR	Infrared Light
IUCN	International Union for the Conservation of Nature
KSWS	Khlong Saeng Wildlife Sanctuary
MBNP	Meru Betiri National Park
MCMC	Markov Chain Monte Carlo
NDVI	Normalized Difference Vegetation Index
NGO	Non-governmental Organisation
NP	National Park
NPA	National Protected Area
NTFC	Northern Tenasserim Forest Complex
PA	Protected Areas
PF	Protected Forest
PPWS	Phnom Prich Wildlife Sanctuary
PR	Pasir Raja Selatan Forest Reserve
PVA	Population Viability Analysis
SaWS	Salakpra Wildlife Sanctuary
SCR	Spatially explicit Capture-Recapture
SMART	Spatial Monitoring And Reporting Tool
SWS or SrWS	Srepok Wildlife Sanctuary
TNNP	Taman Negara National Park
UNESCO	United Nations for Education, Science and Culture
WCS	Wildlife Conservation Society
WEFCOM	Western Forest Complex
WS	Wildlife Sanctuary
WWF	World Wildlife Fund
ZSL	Zoological Society of London

CHAPTER 1

General Introduction

1.1 Tropical forests and large carnivores - challenges to their conservation

Despite covering less than 10% of Earth's land surface, tropical forests harbour the largest living biomass and contain one of the highest levels of biodiversity, including at least two-thirds of the world's terrestrial species (Bradshaw *et al.*, 2009, Giam, 2017). However, the tropics also are where the majority of the world's most threatened biodiversity hotspots are found (Bradshaw *et al.*, 2009). The human population growth and associated impacts, such as habitat loss and overhunting, have devastating effects on biodiversity and are the main cause of the widespread and rapid declines of wildlife worldwide (Cardillo *et al.*, 2004, Ceballos *et al.*, 2015, Ripple *et al.*, 2019). Extinction rates from overexploitation and habitat loss are particularly acute in the tropics, and especially so for terrestrial mammals in tropical forests (Bradshaw *et al.*, 2009, Ripple *et al.*, 2016, Schipper *et al.*, 2008).

Large carnivores are at most at risk of extinction, driven not only by extrinsic factors but facilitated by intrinsic biological traits (Cardillo *et al.*, 2005, Wolf and Ripple, 2017). At a high trophic level, and having low densities, low reproductive rates, large body sizes, and high prey requirements, many large carnivores are among the most threatened mammals worldwide (Cardillo *et al.*, 2005, Dalerum, 2013, Schipper *et al.*, 2008). Large carnivores have undergone striking declines in both population size and geographic range (Dickman *et al.*, 2013, Wolf and Ripple, 2017), with 61% of the world's large carnivore species being threatened with extinction (Ripple *et al.*, 2014). These predators are keystone species that play vital roles in ecosystem functioning and stability, and are valuable proxies of species richness (Berger *et al.*, 2001, Gavashelishvili and Lukarevskiy, 2008, Hebblewhite *et al.*, 2005). Consequently, they can serve as useful indicators for conservation efforts, and can act as umbrella species, potentially enhancing the protection of other species and habitats (Estes *et al.*, 2011, Gavashelishvili and Lukarevskiy, 2008).

Large-bodied carnivore species belong to the Canidae, Felidae, Ursidae, and Hyaenidae families, with the first 3 appearing to suffer from the severest range contractions and population declines (Karanth and Chellam, 2009). The Felidae family is represented by at least 38 extant species, which can differ in body size by over three orders of magnitude, from the small Rusty-spotted Cat (*Prionailurus rubiginosus*, approx. 1 kg) to the Amur Tiger (*Panthera tigris altaica*, 200-325 kg; Carbone *et al.*, 1999). Wild felids naturally occur on all continents except Australasia and Antarctica (Macdonald *et al.*, 2010), and occupy a wide range of habitats. However, several of these obligate carnivores evolved within specialized niches, making them particularly susceptible to environmental changes (Macdonald *et al.*, 2010). Because only a small proportion (<9% for most species) of the range of wild felids is protected (Nowell and Jackson, 1996, Ray *et al.*, 2005), the survival of these species is not guaranteed (Macdonald *et al.*, 2010).

Felids in the *Panthera* genus (i.e., big cats or large felids) are particularly prone to steep population declines, due to their large land and high prey requirements (Wolf and Ripple, 2017). The loss or decline of apex carnivores, such as the big cats, can alter numbers and distributions of mesocarnivores and prey, thereby causing trophic cascades and ecosystem regime shifts (Estes *et al.*, 2011, Ripple and Beschta, 2006, Ripple and Beschta, 2007, Ripple *et al.*, 2014). It is therefore imperative to understand the ecological requirements and threats at the species level for the members of this genus to help develop effective preventive and mitigation strategies that would aid their long-term survival. However, studying these species can be a challenging endeavour due to their secretive nature, low densities, and wide ranges (O'Connell *et al.*, 2011). Consequently, several of the current conservation efforts for big cats are hampered by a lack of knowledge.

1.2 Leopard *Panthera pardus* ecology

The Leopard 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 (Stein and Hayssen, 2013), ranging from alpine areas and boreal forests with lows of -30˚C, to tropical forests and deserts with highs of 70˚C (Hunter and Barrett, 2011). The Leopard consumes a wide range of prey, having

the broadest diet of the large obligate carnivores, with over 90 prey species recorded in sub-Saharan Africa (Hayward *et al.*, 2006). The behavioural plasticity of the Leopard allows it to persists in areas where other carnivores have perished, including within and near major cities such as Johannesburg (Kuhn, 2014) and Mumbai (Odden *et al.*, 2014). Leopard is the apex predator in several areas where Tiger and Lion (*Panthera leo*) have been extirpated, thus playing a vital ecological role as the lone remaining apex large felid in many ecosystems (Balme *et al.*, 2010a, Henschel *et al.*, 2008).

The female Leopard weighs around 35 kg on average, and male Leopard about 65 kg (Kingdon and Hoffmann, 2013), but there is great variation in size within the species, presumably due to regional differences in prey size (Martins *et al*., 2011). In general, a Leopard requires about 5 kg of prey per day (Bailey, 1993, Stander *et al.*, 1997), killing up to 60 large animals per year in order to meet its energetic requirements (Schaller, 1972). The Leopard is mainly solitary, territorial, and has a polygynous mating strategy (Bailey, 1993). Females often defend exclusive home ranges against other unrelated females, whereas males have larger home ranges with largely exclusive core areas that overlap the home ranges of several females. In general, females establish territories adjacent to or within the mother's range, and this kin spatial tenure can in some cases last several generations (Balme and Hunter, 2013). In contrast, males tend to disperse and become transients till they can secure defendable territories, which can take a relatively long time to acquire (Bailey, 1993, Balme *et al.*, 2009). Female Leopard territoriality likely is to secure a minimum prey base, whereas male territoriality likely is to obtain access to multiple females. In accordance, the density of the species has been correlated to prey biomass (Hayward *et al.*, 2006, Henschel *et al.*, 2011).

Several studies have shown the use of olfactory and auditory stimuli by Leopard to advertise its presence, and thus facilitate conspecific avoidance (e.g., Bailey, 1993; Schaller, 1972). Male Leopard territoriality can reduce infanticide (i.e., cubs killed by other males; Balme *et al.*, 2010), and considering that the Leopard has one of the highest infanticide rates recorded in mammalian carnivores (accounting for over a third of cub mortality; Balme and Hunter, 2013), territorial males can play vital roles in maintaining stability and recruitment of the populations. The Leopard likely is susceptible to infanticide due to the lack of cooperative defence (Packer *et al.*, 2009), relatively long periods of cub dependency (Balme and Hunter, 2013), and high levels of sexual dimorphism

(Kingdon and Hoffmann, 2013), which results in females being unable to protect their cubs from larger males. Infanticidal species, such as Leopard, are especially impacted by population disturbances (Packer *et al.*, 2009), as these can result in persistent infanticide and low recruitment rates.

1.3 Leopard conservation

The remarkable adaptability of the Leopard, the relatively high number of confirmed subspecies (*n* = 9), and its broad geographic range, have contributed to a misconception that it is relatively common across its range. Although widely regarded as such in many areas, the Leopard has experienced severe declines in distribution and numbers, because of increased poaching for the illegal wildlife trade, prey declines, conflict with humans, poorly managed trophy hunting, excessive harvesting for ceremonial use of skins, and habitat loss, with the relative importance of these factors varying among regions (Stein *et al.*, 2016). Consequently, the Leopard has lost three-fourths of its historical range (Jacobson *et al.*, 2016), and now occurs in mostly small and fragmented populations, leading to its recent uplisting as Vulnerable by the IUCN (Stein *et al.*, 2016). In Asia a disproportionally high (83-87%) range loss has occurred (Jacobson *et al.*, 2016), and 5 of 8 subspecies are listed as Endangered or Critically Endangered (Stein *et al.*, 2016), some of which have lost as much as 98% of their historical range (e.g., *Panthera pardus nimr*; Jacobson *et al.*, 2016). In addition, a recent review recommended the north Chinese Leopard (*P. pardus japonensis*) be listed as Critically Endangered (Laguardia *et al.*, 2017), leaving only two subspecies in Asia with presumably high and stable numbers: the Indian Leopard (*P. pardus fusca*) and Indochinese Leopard (*P. pardus delacouri*).

Although recent efforts have been made to improve knowledge about the Leopard, empirical field data are still lacking (Stein and Hayssen, 2013). This is especially true in Southeast Asia, where the ecology and conservation status of the species are virtually unknown across large areas of the region.

1.4 The Leopard in Southeast Asia: an understudied and a threatened cat in a fast developing region

Southeast Asia is a well-known global hotspot for endemism and biodiversity (de Bruyn *et al.*, 2014). This region, constituted by the nation-states Brunei, Cambodia, East Timor, Indonesia, Laos, Malaysia, Myanmar, Philippines, Singapore, Thailand and Vietnam (Figure 1.1; Nevins and Peluso, 2008), has the highest global diversity for a number of taxa (Hughes, 2017b). Nevertheless, Southeast Asian biodiversity has been understudied, and the level of taxonomic uncertainty may be significantly higher here than in other parts of the world (Hughes, 2017a).

With over half a billion people and their pressures on biodiversity, Southeast Asia is also one of the most biologically threatened regions worldwide, supporting more threatened species than any other continental area (Duckworth *et al.*, 2012, Hughes, 2017b). In fact, vertebrate extinction risks are the highest in this region (Duckworth *et al.*, 2012), and it is considered the global hotspot of threats to mammals (Hughes, 2017a, Schipper *et al.*, 2008). The ecosystems and species across Southeast Asia are particularly threatened when compared to other tropical regions. However, the conservation challenges of Southeast Asia, the third most populous geographical region of the world, do not arise solely because of the high human density, and the difficulties in reconciling landscape-level conservation with human-space requirements. This is evidenced by the fact that nearby India is notably more successful at conserving species, despite its larger human population (Duckworth *et al.*, 2012).

Southeast Asian wildlife and ecosystems are at particular peril due to a large array of factors that act in synergism and that vary geographically and in intensity. The wider region has some of the highest deforestation rates of all tropical regions, with much of it inside protected areas (Heino *et al.*, 2015), and the rate is still increasing (Grogan *et al.*, 2019, Kim *et al.*, 2015), with several ecosystems and species under imminent threat. For example, from 2000 to 2012, Indonesia, Malaysia and Cambodia had some of the highest rates of forest loss in the world (Hansen *et al.*, 2013). Some countries of the region have already lost over half of their original forest cover (e.g., >93% of forest cover loss in the Philippines), and projections predict as much as 98% forest loss within the coming decade for some countries of the region (Hughes, 2017b). The area of primary and 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, between 2000 and 2010 (Wilcove *et al.*, 2013). More recently, wood pulp and biofuels were added to the list of agroforestry types, all of which are replacing forests at a much higher percentage than any other part of the world (Hughes, 2017b). Deforestation in the region also is being driven by land conversion to other types of croplands (Zeng *et al.*, 2018). Because <10% of Southeast Asian forests are under some form of protection, and prices of commodities, including luxury wood, palm oil, and rubber are expected to increase, habitat loss in the region is expected to continue and have increasingly negative impacts on biodiversity (Grogan *et al.*, 2019, Sodhi *et al.*, 2010).

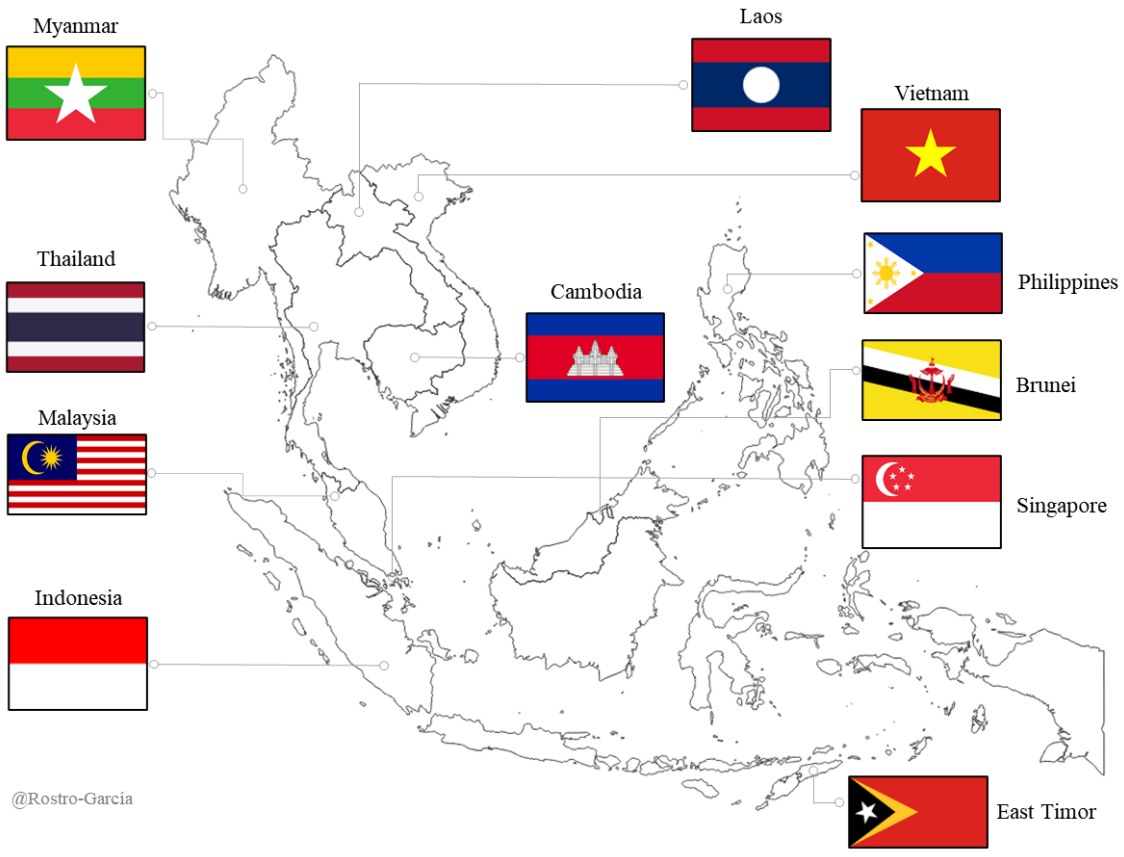


Figure 1.1 Map depicting the location of the different nation-states that constitute Southeast Asia.

The unprecedented rates of deforestation have coincided with the highest mining rates of the tropics, as well as some of the largest numbers of existing and proposed infrastructure projects (Hughes, 2017b). These activities not only result in further habitat fragmentation and other

environmental damages (e.g., through heavy metal leakages), but they likely facilitate the increasing illegal wildlife trade in the region. For example, road development, which has dramatically increased in Southeast Asia, is a catalyst for direct and negative impacts on wildlife, particularly large-bodied mammals such as Leopard (Clements *et al.*, 2014a). Amongst other impacts, these extraction and infrastructure projects can restrict animal movements and promote human encroachment into protected areas. As a result of these and other factors, Southeast Asia is suffering from some of the highest levels of landscape degradation and destruction of the global biodiversity hotspots (Hughes, 2017a).

The above pressures occur alongside a severe and direct threat to wildlife: poaching. Compared to other continental areas, poaching is particularly severe in Southeast Asia, and it currently constitutes the greatest menace to wild vertebrates (Gray *et al.*, 2018). High hunting pressures to meet a large and increasing demand of wildlife products are reaching industrial-scale levels, with indiscriminate snaring rapidly expanding throughout the region (Gray *et al.*, 2018, Tilker *et al.*, 2019). In Southeast Asia, protected and non-protected areas alike are experiencing exceptionally high levels of poaching, primarily to supply the insatiable demand of the ever-growing local, regional, and international wildlife markets. This demand of wildlife parts for medicinal, consumption or ornamental purposes has been driven by an increased perception that these products offer status and wealth, and is causing serious declines in many species (Duckworth *et al.*, 2012, Gray *et al.*, 2018, Lynam, 2010). The effects that poaching incur on wildlife are further exacerbated by the ongoing habitat transformations, and the summation of these overarching threats has led to a widespread defaunation across much of the region (Gray *et al.*, 2018, Tilker *et al.*, 2019).

The accelerated pace of development, the infrastructural growth, the recent explosion of the illegal wildlife trade, and the unsatiable global demand of certain products such as palm oil, rubber, cement, and timber, are generating unprecedented pressures on ecosystems and species of Southeast Asia and are expected to continue or increase as industries become increasingly commercialized (Grogan *et al.*, 2019, Tilker *et al.*, 2019). Consequently, some of the most iconic species of Asia (e.g., Tiger and Rhinoceros *Rhinoceros sondaicus*) have become extirpated in many areas of the region during recent years (Brook *et al.*, 2014, Lynam, 2010). The overall prognosis for the wider

region and the biodiversity therein are becoming increasingly bleak. If the current trends are to continue, many Southeast Asian species will become extinct during the next human generation (Bennett, 2011). Amongst the species most vulnerable to the effects of these rapid drivers of species loss, and thus at a higher risk of regional extinction, are hunting-sensitive species, regional endemics, and large-ranging species (Hughes, 2017b).

Therefore, area and species-specific prioritizations and actions are urgently required before these drivers cause further ecosystem destruction and species loss, and the empty forest syndrome becomes progressively more manifest across Southeast Asia. However, the lack of baseline data to examine trends, the limited number of surveys and inventories (spatially and taxonomically), and the high uncertainty levels about species numbers and distributions, make conservation prioritization and actions highly challenging. For example, the ecology and conservation status of the Leopard, a hunting-sensitive, large-ranging species, are little known across Southeast Asia. In fact, hardly anything is known about the species in most Southeast Asian countries, despite Leopard being the apex predator in several areas where other large carnivores, such as Tiger, have been extirpated. The lack of information on the species in large parts of its distribution likely stem from the difficulty of studying this elusive, forest-dwelling species in a region of rapid development and marked by political instability in some areas. Nevertheless, the successful conservation of the Leopard in Southeast Asia requires the collection of a multifaceted set of data, including population status, ecological requirements, as well as human activities and their influence on Leopard populations. Two subspecies of Leopard occur in Southeast Asia, the Indochinese and Javan (*P. pardus melas*) Leopard, for which such information is urgently needed.

1.5 The Indochinese Leopard

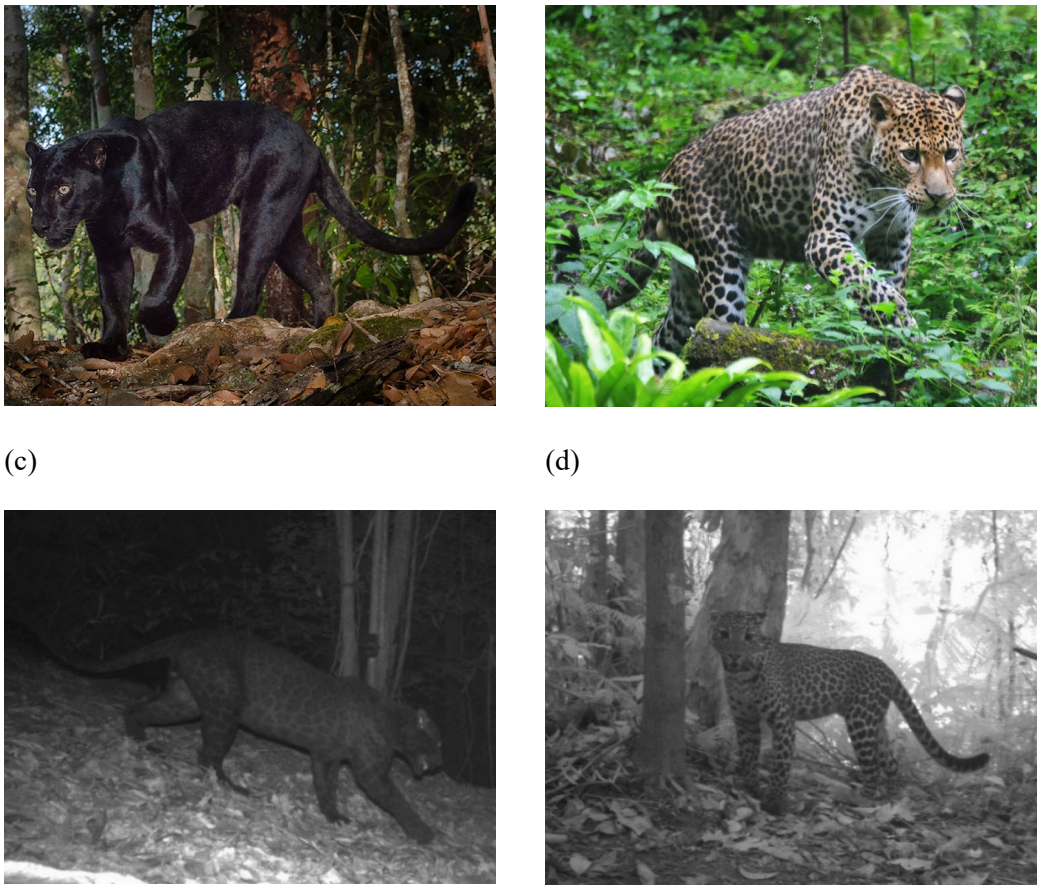
The Indochinese Leopard is a genetically distinct subspecies (Miththapala *et al.*, 1996, Sugimoto *et al.*, 2014, Uphyrkina *et al.*, 2001) that historically occurred throughout all mainland Southeast Asian countries and southeastern China (hereafter Southeast Asia). The exact historical geographical boundary of this subspecies is unclear, but it is presumed to have occurred from the India-Myanmar border to Vietnam and from Singapore to southeastern China, as far north as the Pearl River (Rostro-

García *et al.*, 2016a). 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. Additionally, basic ecological data on this subspecies are lacking. For example, by the time this study commenced, only two peer-reviewed articles estimated Indochinese Leopard densities using spatially explicit capture-recapture (SCR) models (Gray and Prum, 2012, Hedges *et al.*, 2015), and dietary studies only came from one region in western Thailand (Grassman, 1999, Rabinowitz, 1989). Clearly, a range-wide assessment is necessary to confirm the status of this subspecies, and more ecological information required to determine the role of this important apex carnivore in the ecosystems.

1.6 The Javan Leopard

The Javan Leopard, the most morphologically and genetically distinct Leopard subspecies, is confined to the Indonesian island of Java and is classified as Critically Endangered by the IUCN (Ario *et al.*, 2008). This Leopard subspecies historically occurred widely throughout the island of Java (Gerngross, unpubl. data; Hoogerwerf, 1970), and presumably on the Kangean islands (Jacobson *et al.*, 2016), but currently its distribution is highly fragmented and limited to Java. Major ongoing threats to the subspecies are human population growth, direct killing, and habitat loss (Ario *et al.*, 2008, Jacobson *et al.*, 2016). Java, the most populous island in the world with one of the densest human populations (over 1,100 people/km^2), had lost >90% of its natural habitat by the early 1990's (Santiapillai and Ramono, 1992). Currently, the Javan Leopard has the smallest proportion of core habitat of all Leopard subspecies, with only 3% of core habitat remaining (Jacobson *et al.*, 2016), suggesting that this subspecies is at a greater risk of extinction compared to other Leopard subspecies. However, less than 10 peer-reviewed articles have been published on this subspecies, out of which only one was an applied article (Jacobson *et al.*, 2016). By the time this study commenced, no published paper estimated the density of this subspecies using SCR models.

(a) (b)



(c) (d)

Figure 1.2 Photographs of a: (a) melanistic Indochinese Leopard (*Panthera pardus delacouri*), and (b) Javan Leopard (*Panthera pardus melas*), by Paul Thompson Wildlife Photography and ZooChat, respectively. Camera-trap pictures from this study of a: (c) melanistic Indochinese Leopard, and (d) Javan Leopard.

Despite the precarious state of these Leopard subspecies, their ecology has been little studied. The profound lack of information in large parts of their distribution hinders the implementation of appropriate interventions, and to date, effective efforts to protect these Leopard subspecies are lacking. However, as threats to Leopard survival become manifold in Southeast Asia, urgent assessment of the population status in the region is required, so that immediate conservation actions can be devised. Consequently, this study aims to provide baseline information on the population status and ecology of the Leopard in key areas throughout Southeast Asia, which would allow an

assessment of the species' conservation status and help identify major threats to its persistence in the wider region.

1.7 Thesis Overview

1.7.1 Broad research aims

The primary purpose of the study is to collect ecological information with an applied, conservation-oriented intent. Specifically, this thesis has two overarching aims:

1. To characterise and quantify Indochinese and Javan Leopard populations in areas within their current distribution in Southeast Asia
2. To identify the ecological parameters that determine Leopard presence in key populations in Southeast Asia

A secondary purpose of the study is analytical-practical, aiming to examine current practices, and apply novel approaches to study the Leopard. Overall, this study aims to provide baseline information on the population status and ecology of the Leopard in Southeast Asia, as well as identifying major threats to the species in the region. Such information contributes to the scientific knowledge necessary for informed conservation efforts, and provides a benchmark against which future studies can be compared.

1.7.2 Thesis Outline

This body of work is presented as an integrated thesis, which alongside this Introduction, contains 5 data chapters, followed by a closing general discussion chapter. Data chapters are formatted as journal articles, each with its own appendices. Figures, tables, and appendices are presented at the end of each corresponding chapter and can be accessed through hyperlinks. A combined list of references is presented at the end of the dissertation. The thesis is followed by 7 appendices that comprise additional publications which used data collected for my DPhil. The data chapters are presented in the form of independent manuscripts from Chapters 2 to 6, and some level of repetition is therefore unavoidable:

Chapter 2 - Endangered Leopards: Range collapse of the Indochinese Leopard in Southeast Asia

The aim of this chapter was to determine the current distribution of the Indochinese Leopard, and broadly estimate its population size, by reviewing data from camera trap and other wildlife surveys conducted in the region during the past 20 years. In addition, this chapter aimed to identify major strongholds and priority sites for the subspecies.

Authors: S. Rostro-García (SR-G), J. F. Kamler (JFK), E. Ash (EA), G. R. Clements (GRC), L. Gibson (LG), A. J. Lynam (AJL), R. McEwing (RM), H. Naing (HN), S. Paglia (SP).

Contributions: SR-G led the conceptualization, data collection, curation, and analyses, with input from JFK. SR-G wrote the initial manuscript. EA, GRC, LG, AJL, RM, HN and SP provided important unpublished data. All authors revised the manuscript and gave final approval for publication.

[Published - Biological Conservation, 2016 (201): 293-300].

Chapter 3 - Leopards in Southeast Asia: Critically Endangered but understudied big cats in a fast developing region

The population status of the Indochinese and Javan Leopard in Southeast Asia are mostly unknown, yet urgent, on-the-ground assessments are required to guide conservation action as threats to Leopard persistence are becoming manifold in the region. The aim of this chapter was to elucidate the status of the Leopard in the region, by conducting the largest ever camera-trap survey for Leopard in Southeast Asia. Specifically, the densities, activity patterns, and habitat use of the species were estimated in several key populations across Southeast Asia, including in areas identified as priority sites in Chapter 2. The findings of this study represent the first quantitative assessment of the status of the species in the region, and provide relevant information for evidence-based conservation actions. This study also provides important baseline data for key Leopard populations, thereby creating a benchmark against which future estimates can be compared.

Authors: S. Rostro-García (SR-G), J. F. Kamler (JFK), R. Sollmann (RS), G. Balme (GB), A. Godfrey (AG), S. Saosoong (SS), K. Siripattaranukul (KS), W. Thomas (WT), R. Sookmasuang (RSk), R. Crouthers (RC), V. In (VI), S. Prum (SP), G. R. Clements (GRC), S. H. Liang (SHL), A. K. B. A. Hashim (AKBAH), R. Avriandy (RA), D. Gunaryadi (DG), N. Kholiq (NK), K. Indarto (KI), D. W. Macdonald (DWM).

Contributions: SR-G led the conceptualization, data collection, curation, and analyses, with input from RS and JFK. SR-G wrote the initial manuscript. AG, SS, KS, WT, RSk, RC, VI, SP, GRC, SHL, AKBAH, RA, DG, NK, KI provided support with fieldwork. GB and DWM secured funding. RS, JFK, and DWM reviewed the manuscript.

[Submitted to Biodiversity and Conservation].

Chapter 4 - Camera trapping in low-density populations: can we get reliable density estimates?

Despite the widespread adoption of SCR methods to estimate population parameters and the importance of appropriate sampling designs, little guidance exists on how to practically implement SCR studies to generate reliable estimates, and their performance in low-density populations remains little understood. In this chapter, simulated and empirical data under a range of ecologically realistic scenarios and commonly used study designs were used to investigate the performance of SCR models in low-density populations surveyed using camera traps. The Leopard, one of the most studied species using camera traps, was used as a case study. Study design recommendations are given to facilitate the applicability of SCR methods when studying low-density populations.

Authors: S. Rostro-García (SR-G), M. Kéry (MK), M. Meredith (MM), R. Sollmann (RS), J. F. Kamler (JFK), G. Balme (GB), A. Godrey (AG), S. Saosoong (SS), K. Siripattaranukul (KS), W. Thomas (WT), R. Sookmasuang (RSk), R. Crouthers (RC), T. Gharajehdaghipour (TG), V. In (VI), S. Prum (SP), D. W. Macdonald (DWM).

Contributions: SR-G led the conceptualization, data collection, curation, and analyses with input from MK and MM. SR-G wrote the initial manuscript. AG, JFK, SS, KS, WT, RSk, RC, TG, SP,

and VI provided support with fieldwork. GB and DWM secured funding. RS, JFK, and DWM reviewed the manuscript.

[In preparation for journal submission].

Chapter 5 - An adaptable but threatened big cat: density, diet and prey selection of the Indochinese Leopard (*Panthera pardus delacouri*) in eastern Cambodia

The Indochinese Leopard was studied in Srepok Wildlife Sanctuary (SWS), Cambodia, a globally important site for the subspecies and one of the last remaining viable populations in Southeast Asia. Specifically, the objectives of this chapter were to: (i) estimate the density of Leopard; (ii) determine the diet and prey selection of the species, with a focus on differences between males and females; and (iii) determine predation impact of Leopard on the community of threatened ungulate species. In order to meet the objectives, DNA confirmed scats, camera-trap and line-transect data were used. Overall recommendations for the conservation of the subspecies in this priority sites are given, and the implications of the findings are discussed.

Authors: S. Rostro-García (SR-G), J. F. Kamler (JFK), R. Crouthers (RC), K. Sopheak (KS), S. Prum (SP), V. In (VI), C. Pin (CP), A. Caragiulo (AC), D. W. Macdonald (DWM).

Contributions: SR-G led the conceptualization and designed the study with input from DWM. SR-G led the data collection, curation, and analyses, with input from JFK. AC carried out the molecular laboratory work. RC obtained prey densities. RC, KS, SP, VI, and CI provided support in the field. SR-G wrote the initial manuscript. All authors revised the manuscript and gave final approval for publication.

[Published - Royal Society Open Science, 2018 (5): 171187].

Chapter 6 - Fading spots: Population dynamics of the last Leopard population of eastern Indochina

The Leopard population in eastern Cambodia represents the last remaining viable population of eastern Indochina, and one of three priority sites for Indochinese Leopard conservation in Southeast

Asia. However, reliable information is currently lacking on population status and trend, both of which are critical to assess conservation status, determine effectiveness of current management practices, and guide conservation actions. In this chapter, open-population SCR models were used to estimate density, survival, recruitment, and population growth rates of the Indochinese Leopard in SWS using data from 7 systematic camera-trap surveys conducted over 11 years, in the first-ever study of Leopard population dynamics in Asia. The effectiveness of management practices is discussed, and both implications and recommendations for Leopard conservation in the wider region are provided.

Authors: S. Rostro-García (SR-G), B. C. Augustine (BCA), M. Kéry (MK), J. F. Kamler (JFK), R. Sollmann (RS), G. Balme (GB), R. Crouthers (RC), T. N. E. Gray (TNEG), M. Groenenberg (MG), V. In (VI), S. Prum (SP), D. W. Macdonald (DWM).

Contributions: SR-G led the conceptualization and data collection with input from JFK. SR-G led the data curation and analyses with input from BCA and MK. SR-G wrote the initial manuscript. RC, TNEG, MG, VI, and SP provided support with fieldwork. GB and DWM secured funding. RS, JFK, and DWM reviewed the manuscript.

[Submitted to Conservation Biology].

Chapter 7 - General Discussion

This chapter summarises and discusses the findings from the dissertation. In addition, methodological considerations, study limitations, possibilities for future studies, and implications for Leopard conservation and research in Southeast Asia are provided.

Authors: S. Rostro-García.

Contributions: SR-G wrote the initial manuscript. RS, JFK, and DWM reviewed the manuscript.

1.7.3 Additional Research

The following list summarises additional papers that I contributed to which included data collected for my DPhil:

Rostro-García, S., Kamler, J. F., Clements, G. R., Lynam, A. J. & Naing, H. 2019. *Panthera pardus* ssp. *delacouri*. *The IUCN Red List of Threatened Species 2019: e.T124159083A124159128*. https://www.iucnredlist.org/species/124159083/163986056. [Appendix A]

Rostro-García, S.; Kamler, J. F.; Minge, C.; Caragiulo, A.; Crouthers, R.; Groenenberg, M.; In, V.; Pin, C.; Sovanna, P; Gray, T. N. E.; Kéry, M.; Macdonald, D. W. 2021. Small cats in big trouble? Diet, activity, and habitat use of jungle cats and leopard cats in threatened dry deciduous forest, Cambodia. *Ecology and Evolution*, 11, 4205-4217. [Appendix B].

Clements, G. R., **Rostro-García, S.**, Kamler, J. F., Liang, S. H., & Hashim, A. K. B. A. 2021. Conservation status of large mammals in protected and logged forests of the greater Taman Negara Landscape, Peninsular Malaysia. *Biodiversitas*, 22, 272-277. [Appendix C].

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CHAPTER 2

Endangered Leopards: range collapse of the Indochinese Leopard (*Panthera pardus delacouri*) in Southeast Asia

2.1 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 973-2,503 individuals, with only 409-1,051 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.

Keywords: Carnivore conservation, distribution, IUCN status, *Panthera pardus*, population size, wildlife trade.

2.2 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, the Leopard 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 (*P. pardus japonensis*) be listed as Critically Endangered because of the high risk of extinction (Laguardia *et al.*, 2017), leaving only two subspecies in Asia with presumably high and stable numbers: the Indian Leopard (*P. pardus fusca*) and Indochinese Leopard (*P. pardus delacouri*).

The Indochinese Leopard is a genetically distinct subspecies (Miththapala *et al.*, 1996, Sugimoto *et al.*, 2014, Uphyrkina *et al.*, 2001) 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.*, 2017). 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.

2.3 Materials and methods

2.3.1 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 grey literature, especially those by local organisations operating in Southeast Asia that might have conducted wildlife surveys. When necessary, we contacted the authors for additional information. In addition, we directly contacted organisations 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.

2.3.2 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 *et al.*, 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%).

2.4 Results

We reviewed 146 wildlife surveys from 109 sites from 6 countries within the historical range of the Indochinese Leopard (Appendix 2.1), in addition to using previous reviews for southeastern China (Laguardia *et al.*, 2017) 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 (Figure 2.1). 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 973-2,503 total individuals (*N*), with 409-1,051 breeding adults (N_e). Our sensitivity analysis using 10% and 90% occupancy showed that *N* ranged from 162-3,755 total individuals, whereas N_e ranged from 68-1,577 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 2.1). 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 (Figure 2.1; Appendix 2.1). 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 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 2.1). 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 detect Leopard (Appendix 2.1). 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 2.1). Although Leopard was recently detected in Kandal Province, southern Cambodia (Appendix 2.1), we assume this population is not viable due to high levels of habitat degradation and 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.*, 2017; Figure 2.1). Laguardia *et al.* (2017) 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 2,483 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 2.1). 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 Laos and Panthera, unpubl. data; Appendix 2.1). 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 2.1). 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. While 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 2.1). 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; Figure 2.1; Appendix 2.1). Leopard also has been detected in fragmented secondary forests southwest of Kuala Lumpur (Sanei *et al.*, 2011), and other fragmented forests throughout the country (Figure 2.1; Appendix 2.1).

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 2.1). 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 2.1). 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 2.1). 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 (Figure 2.1; Appendix 2.1). The Southern Forest Complex presumably contains the largest viable population of Leopard in the country (Figure 2.1; Appendix 2.1). 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 (Figure 2.1). 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 2.1). 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 2.1). 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 National Park (NP) in northwestern Thailand (Appendix 2.1), 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 *et al.*, 2008). Nevertheless, Leopard was not detected in all PAs within the complex (Appendix 2.1), and its population in Huai Kha Khaeng WS declined 38% over 3 years during the late 1990s (Simcharoen *et al.*, 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 2.1). 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 2.1). 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 2.1). 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 2.1). 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.

2.5 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 (Figure 2.1). 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 (Mondol *et al.*, 2015, Raza *et al.*, 2012) 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 organisations (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.*, 2014a). 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 Leopard (*P. pardus orientalis*; Wildlife Conservation Society Russia Program, 2015), and outbreaks of this disease recently caused a 36% decline in a population of Amur Tiger (*P. 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 Tiger (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 the 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.*, 2012a). 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 steppingstone, 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 >500 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.

2.6 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 973-2,503 individuals remaining with only 409-1,051 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 1,577 individuals, still below the 2,500 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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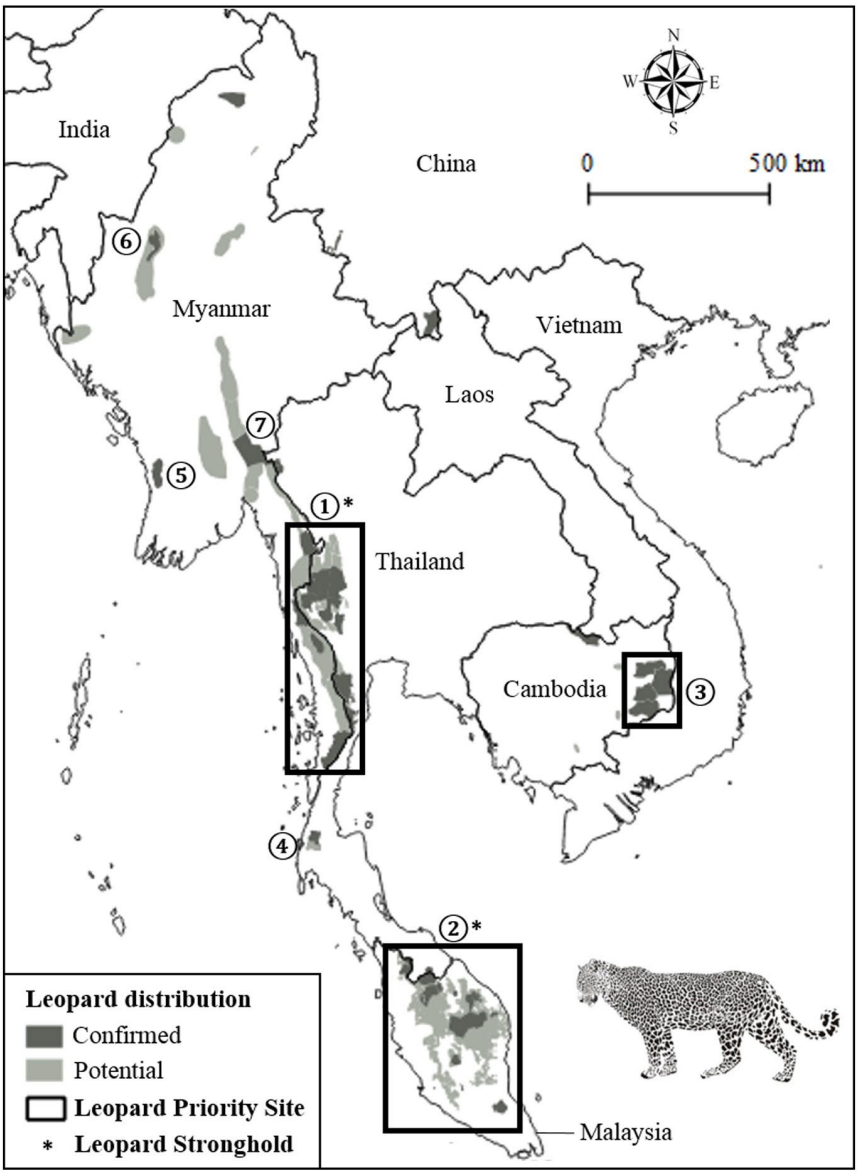


Figure 2.1 The current (confirmed and potential) estimated distribution of the Indochinese Leopard (*Panthera pardus delacouri*) in Southeast Asia. The areas surrounded by rectangles indicate Leopard priority sites: (1) Northern Tenasserim Forest Complex; (2) Peninsular Malaysia, and; (3) Eastern Plains 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 Wildlife Sanctuary; (6) Alaungdaw Kathapa-Mahamyaing Complex, and; (7) northern Karen (Kayin) State.

2.8 Supplementary Material

Appendix 2.1 Data from surveys of Leopard in Southeast Asia. Download:

https://ars.els-cdn.com/content/image/1-s2.0-S0006320716302658-mmc1.xlsx

CHAPTER 3

Leopards in Southeast Asia: Critically Endangered but understudied big cats in a fast developing region

3.1 Abstract

Southeast Asia, a global hotspot for biodiversity and endemism, currently is one of the most biologically threatened regions worldwide, with ecosystems and species experiencing unprecedented anthropogenic pressures. Despite being classified as Critically Endangered, the population status of the Indochinese Leopard (*Panthera pardus delacouri*) and Javan Leopard (*P. pardus melas*) in Southeast Asia are mostly unknown. As threats to Leopard survival become manifold in the region, urgent, on-the-ground assessment is required to inform conservation and management actions. We conducted the largest camera-trap study for Leopard in Southeast Asia, encompassing 7 sites across 4 countries to elucidate the status of the Leopard and estimate densities, activity patterns, and habitat use of the species in key populations across the region. We developed spatially explicit capture-recapture models to estimate Leopard densities, and analysed detections within a Bayesian occupancy framework to evaluate Leopard habitat use in response to environmental and anthropogenic factors. In northern sites (Cambodia, Thailand), Leopard was mostly nocturnal, densities were low (0.23-0.88 Leopard/100 km^2), and its habitat use was strongly positively associated with higher vegetation productivity (measured at 1 km), and moderately negatively associated with preferred prey and forest loss (15 km). In contrast, in southern sites (Malaysia, Indonesia), Leopard was almost exclusively diurnal, densities were higher (0.97-4.74 Leopard/100 km^2), and its habitat use was strongly positively associated with preferred prey, and moderately positively associated with human presence and forest loss (15 km). The Leopard densities estimated in our study areas are some of the lowest ever reported for the species, with illegal human activities appearing to affect densities, habitat use and activity patterns of Leopard. The effects of humans differed between northern and southern sites, likely due to differences pertaining to poaching, which appears to be influenced by religious beliefs, socio-economic status, and proximity to major wildlife

consuming markets. Our findings suggest the overall prognosis of the species in the region is becoming increasingly bleak, and only with the implementation of timely, effective, and area-specific strategies will the long-term conservation of Leopard be feasible in Southeast Asia.

Keywords: Bayesian analysis, camera trapping, density, habitat use, Indochinese Leopard, Javan Leopard, occupancy model, *Panthera pardus delacouri*, *Panthera pardus melas*, Southeast Asia, spatial capture-recapture.

3.2 Introduction

The Leopard (*Panthera pardus*) has the widest distribution of any felid species (Stein and Hayssen, 2013), and the broadest diet of all large carnivores (Hayward *et al.*, 2006). Despite its adaptability in habitat use and diet, the Leopard has experienced severe declines in distribution and numbers, and currently occupies only 25-37% of its historical range (Jacobson *et al.*, 2016), leading to its recent uplisting as Vulnerable by the IUCN (Stein *et al.*, 2016). The primary reasons for the decline are habitat loss, prey depletions, conflict with humans, and poaching for the illegal wildlife trade, with the relative importance of these factors varying among regions (Jacobson *et al*., 2016; Stein *et al*., 2016). Consequently, the Leopard now occurs in mostly small and fragmented populations, especially in Asia where a disproportionally high range loss (83-87%) has occurred (Jacobson *et al.*, 2016), and where 7 of 8 subspecies are either already listed or petitioned to be listed as Endangered or Critically Endangered.

In order to provide a baseline for future monitoring and guide science-based recovery efforts, quantitative information is required to identify the factors that influence Leopard occurrence and abundance. However, such information is limited, particularly in Southeast Asia where the ecology and conservation status of the Leopard are virtually unknown. Nonetheless, this region, characterised by some of the world's fastest growing, and most dynamic economies is one of the most biologically threatened regions worldwide, supporting more threatened species than any other continental area (Duckworth *et al.*, 2012, Hughes, 2017). The accelerated pace of development, the infrastructural growth, the explosion in the illegal wildlife trade, and the extraordinary deforestation rates to supply an insatiable global demand for products such as palm oil, rubber, and timber, are generating unprecedented pressures on ecosystems and species of Southeast Asia, and are expected to continue or increase as industries become increasingly commercialized (Grogan *et al.*, 2019, Tilker *et al.*, 2019). Poaching, mostly using snares and largely to supply the ever-expanding local, regional and global markets for wildlife products (e.g., bushmeat, medicine, ornamentation, pets), has been particularly severe in Southeast Asia, and currently represents the greatest threat to wildlife (Gray *et al.*, 2017). Alongside habitat destruction, this significant, yet often overlooked pressure, is causing defaunation across much of the region and placing it into the midst of a conservation crisis.

Consequently, some of the region's most iconic species, such as Tiger (*Panthera tigris*) and Sumatran Rhinoceros (*Dicerorhinus sumatrensis*), have been locally extirpated over vast areas, while many others have been negatively affected by these anthropogenic impacts (Duckworth *et al.*, 2012, Lynam, 2010), including the Leopard (Rostro-García *et al.*, 2018).

Despite being the apex predator in several areas where other large carnivores have been extirpated, little is known about the Leopard in most Southeast Asian countries. This lack of information partly stems from the difficulty of studying populations of this elusive species in the Tropical and Subtropical Moist Broadleaf Forest of Southeast Asia, which are unique for harbouring high frequencies of melanistic individuals (da Silva *et al.*, 2017). The occurrence of melanism hinders the visibility of the spot patterns in camera-trap photographs, which in turn represents an exceptional challenge for identifying individuals, and thus estimating and monitoring populations. Nevertheless, the successful conservation of Leopard in Southeast Asia requires the availability of a multifaceted set of information, including population status, ecological needs, and influence of prevailing human activities on Leopard populations. Two Critically Endangered subspecies of Leopard that exhibit melanism occur in this region, the Indochinese Leopard (*P. pardus delacouri*), and Javan Leopard (*P. pardus melas*), for which such information is urgently required (Rostro-García *et al.*, 2019, Stein *et al.*, 2016).

The Indochinese Leopard is a genetically distinct subspecies (Miththapala *et al.*, 1996, Sugimoto *et al.*, 2014, Uphyrkina *et al.*, 2001) that historically occurred throughout all mainland Southeast Asian countries and southeastern China (Nowell and Jackson, 1996). However, this subspecies has experienced severe demographic and geographic range contractions, and now occurs in only a small fraction (about 2-6%) of its historical range. The Indochinese Leopard has been extirpated in Singapore, likely extirpated in Laos and Vietnam, nearly extirpated in Cambodia and China, and has greatly reduced distributions in Thailand, Myanmar, and Malaysia (Rostro-García *et al.*, 2019). Consequently, the subspecies recently was classified as Critically Endangered by the IUCN (Rostro-García *et al.*, 2019). Rostro-García *et al.* (2016a) identified three priority sites for Indochinese Leopard conservation in Southeast Asia: 1) the Northern Tenasserim Forest Complex on the Thailand-Myanmar border, 2) Peninsular Malaysia, and 3) eastern Cambodia. However, up-

to-date density estimates are required to determine the current status of the subspecies in these important sites.

The Javan Leopard, the most morphologically and genetically distinct of all Leopard subspecies, is confined to the Indonesian island of Java and is classified as Critically Endangered by the IUCN (Ario *et al.*, 2008). This subspecies historically occurred widely throughout Java (Jacobson *et al.*, 2016), but its current distribution is highly fragmented and restricted on the island, which has one of the highest human population densities in the world. The Javan Leopard, the island's only remaining large felid, has one of the smallest proportions of core habitat of all Leopard subspecies, with only 3% of core habitat remaining (Jacobson *et al.*, 2016). Surprisingly, few peer-reviewed articles on this Critically Endangered subspecies have been published, and only three national parks have been identified to potentially support more than 50 individuals (Jacobson *et al.*, 2016, Wibisono *et al.*, 2018).

In spite of the precarious state of both Leopard subspecies, effective conservation efforts to protect them are lacking, and information essential to help guide effective conservation actions has not been acquired. As threats to Leopard survival become manifold in Southeast Asia, urgent on-the-ground assessment of the population status in the region is required. Therefore, the purpose of this study was to determine the current population status of the Leopard and the ecological correlates that predict its habitat use and abundance within important sites in Southeast Asia. We used camera-trapping data from 7 sites across 4 countries, including all 3 of the priority sites identified for the Indochinese Leopard (Rostro-García *et al.*, 2016a) and an essential site identified for the Javan Leopard. We estimated the densities of Leopard in these key populations across a gradient of habitat and anthropogenic disturbances. In addition, we used occupancy modelling, and examined diel activity patterns to assess the relative influences of habitat, prey, and human disturbance on Leopard habitat use and temporal behaviour. This study comprises the largest data set of Leopard in Southeast Asia, and constitutes the first quantitative assessment of the status of the species in the region. Our findings represent important baseline data for key Leopard populations, provide a benchmark against which future estimates can be compared, and produce information necessary for evidence-based conservation actions.

3.3 Materials and methods

3.3.1 Study areas

The study areas for the Indochinese Leopard were chosen based on the results from a recent review that determined the current distribution of the subspecies (Rostro-García *et al.*, 2016a), including some of the last remaining populations found within the three identified priority sites. The study area for the Javan Leopard was selected based on Jacobson *et al.* (2016) and discussions with local conservation organisations. Overall, we investigated density and habitat use of the Indochinese and Javan Leopard were studied in 7 sites within 4 countries over a period of 2 years (Figure 3.1).

Cambodia

The study was conducted in the Eastern Plains Landscape (EPL), Cambodia, which appears to hold the only viable Leopard population of all of Cambodia, Laos, and Vietnam (Rostro-García *et al.*, 2016a, Rostro-García *et al.*, 2019). The EPL contains the only remaining population of Leopard in Southeast Asia where melanistic individuals are absent, and the last remaining Leopard population inhabiting a landscape dominated by open dry deciduous forests (Rostro-García *et al.*, 2016a). This ecosystem harbours the world's largest population of Banteng (*Bos javanicus*, Gray *et al.*, 2012), which a recent study showed is one of the main prey of Leopard (Rostro-García *et al.*, 2018). Research was conducted in two protected areas within the EPL where Leopard previously was detected using camera traps: Srepok Wildlife Sanctuary (SrWS), formerly called the Mondulkiri Protected Forest till 2016, and Phnom Prich Wildlife Sanctuary (PPWS; Figure 3.1). The SrWS (3,730 km^2), the largest protected area in EPL, is dominated by open and dry deciduous dipterocarp forests (ca. 70%) interspersed with small patches of closed evergreen forests (Rostro-García *et al.*, 2021). In contrast, the PPWS (2,225 km^2), notable for its rich habitat diversity, has a mosaic of open deciduous and closed evergreen and semi-evergreen forest patches.

Peninsular Malaysia

In Peninsular Malaysia, one of the two remaining strongholds for the Indochinese Leopard (Rostro-García *et al.*, 2016a), we conducted camera-trap surveys within the Greater Taman Negara

Landscape, located in north-central Peninsular Malaysia. Specifically, surveys were conducted in two study areas: Merapoh, which is situated in the western part of Taman Negara National Park (TNNP) in Pahang state, and Pasir Raja Selatan Forest Reserve (PR), which is part of the Dungun Timber Complex (DTC), located in Terengganu state (Figure 3.1). The TNNP is the largest protected area of the country (4,343 km^2), occurring in three states (i.e., Kelantan, Pahang, Terengganu), and one of the largest in Southeast Asia (Kawanishi and Sunquist, 2004). The TNNP, broadly classified as a tropical evergreen moist forest, contains a large diversity of vegetation types, including lowland dipterocarp forest to upper montane forest, montane oak (Quercoideae) and ericaceous (Ericaceae) forests. Merapoh was systematically camera-trapped in 1999-2000, although Leopard density was not estimated because all individuals were melanistic and the spot-patterns were not visible for individual identification (Kawanishi and Sunquist, 2004). The DTC (1,067 km^2), consists of six permanent forest reserves where logging is permitted, including PR adjacent to the eastern border of TNNP. The DTC follows the tenets of sustainable forest management, and has been compliant with the certification standards from the Forest Stewardship Council (FSC) since 2008, making it one of the few FSC certified logging concessions in Peninsular Malaysia. The DTC, managed by Kumpulan Pengurusan Kayu Kayan Terengganu Sdn. Bhd., consists of dipterocarp forests (lowland mixed, hill and upper hill), and montane forest. The PR, due to its proximity to TNNP, presumably contains a high diversity of species. However, this forest reserve has never been systematically surveyed. Both study areas occur south of the Isthmus of Kra (narrowest part of the Malay Peninsula) where there is a near fixation of melanism in Leopard populations (Kawanishi *et al.*, 2010).

Thailand

In Thailand, surveys were conducted in Salakpra Wildlife Sanctuary (SaWS), the first wildlife sanctuary of the country, and Khlong Saeng Wildlife Sanctuary (KSWS; Figure 3.1). The SaWS (868 km^2) is part of the Western Forest Complex (WEFCOM), which together with the adjacent Southern Forest Complex in Myanmar, comprise the Northern Tenasserim Forest Complex, the largest remaining forest track in mainland Southeast Asia and one of the two remaining Leopard strongholds (Rostro-García *et al.*, 2016a). The SaWS consists of semi-evergreen and dry dipterocarp forests, and

contains a mixed population of spotted and melanistic Leopard. The KSWS (1,155 km^2), located south of the Isthmus of Kra, is part of the Khlong Saeng-Khao Sok Complex, and together with adjacent protected areas form the largest continuous forested area in southern Thailand. The dominant forest type in KSWS is semi-evergreen forest. These wildlife sanctuaries have never been systematically surveyed for Leopard.

Java

The Javan Leopard survey was conducted in Meru Betiri National Park (MBNP, 580 km^2), located in East Java (Figure 3.1). This protected area is part of Belambangan Biosphere Reserve, recently declared as one of the World's Biosphere Reserves by the United Nations for Education, Science and Culture (UNESCO). The MBNP is 1 of only 3 protected areas identified to potentially support more than 50 individuals of this Critically Endangered Leopard subspecies (Wibisono *et al.*, 2018). The MBNP is dominated by lowland tropical forests, with mangrove and swamp forests. The MBNP has never been systematically surveyed for Leopard.

3.3.2 Camera trapping

In each study site, the most remote areas (hereafter core areas) were surveyed using camera traps for approximately 3 months, primarily during the respective 6-month dry seasons (given the difficulties of surveying during the wet season) between December 2015 and November 2017 (Table 3.1). The number of camera-trap stations per study area varied, with an average of 45 stations per study site (range: 26-84; Table 3.1). In general, each station consisted of a pair of camera traps operating 24 hours/day, which were placed on opposite sides of a trail to obtain photos of both flanks of each Leopard, and thus allow for individual identification. Stations were spaced about 2 km apart considering a trade-off between spatial coverage and logistical feasibility. Camera traps were deployed at locations where there were Leopard signs, or places that maximised chances of detecting the species (e.g., animal trails, dirt roads, ridges), as carnivores species have been shown to have significantly higher probability of being detected on these landscape features, relative to random placement during the dry season (Cusack *et al.*, 2015, Sollmann *et al.*, 2011). Cameras were placed

on trees located 1.5-5 m from the middle of the trail, and motion detectors set to trigger at a height of 40-45 cm above the centre of the trail. When possible, stations were checked approximately one month after setting. During these checks, some stations were relocated to nearby locations to reduce risk of theft, flood, or fire. In addition, a few stations were relocated when fresh Leopard sign was found nearby, or when an extremely low detection of mammals occurred in the original location. During our Leopard survey in SaWS, there was a concurrent camera-trap survey for Tiger conducted by ZSL-Thailand, in which stations were placed approximately 4 km apart outside of the core area to cover the entire park. This survey used the same camera model as our survey (see below), during the same period and following the same protocol. Therefore, we included data from these additional stations in our analysis of SaWS.

3.3.3 Melanistic Leopard

Reliable density estimates of species from camera traps are possible only if individuals can be unambiguously identified. In spotted Leopard populations, individual identification is possible because Leopard exhibit individually identifiable characteristics or markings (i.e., unique patterns of rosettes and spots) in the pelage. However, in melanistic populations, the spot patterns typically are indistinguishable under normal light, which makes individual identification extremely difficult. Melanism, defined as the occurrence of individuals whose coloration is darker than the typical form of a species, is inherited as Mendelian, monogenic recessive trait in Leopards (Kawanishi *et al.*, 2010). In contrast to all other Leopard subspecies throughout the world, populations of both Indochinese and Javan Leopard contain a large proportion of melanistic individuals. This is particularly true for populations in mainland Southeast Asia that are south of the Isthmus of Kra, where there is a near fixation of melanism (da Silva *et al.*, 2017, Kawanishi *et al.*, 2010). The predominance of this polymorphism is the primary reason that reliable density estimates of Indochinese and Javan Leopard have not been obtained in most sites in Southeast Asia, despite large amount of incidental data available from numerous camera trapping studies conducted in the region for Tiger (*Panthera tigris*) and other species. The recent application of automated infrared cameras has shown that the more heavily pigmented rosette markings of melanistic Leopard can be visible

when illuminated by infrared light (IR; Kawanishi *et al.*, 2010). This likely is possible due to the physical properties of the eumelanin, as the transmission coefficient of this pigment increases with the increased wavelength of a light source (Hedges *et al.*, 2015). Given that near infrared light, used in camera traps, has a longer wavelength than visible light, it is possible to observe the more heavily pigmented spot-patterns when in contrast with the less pigmented background of the pelage (Figure 3.2). Consequently, on study sites where melanism was expected to occur (SaWS, KSWS, TNNP, and MBNP) we used Panthera cameras developed specifically for this study (Panthera V6 IR; Panthera, New York, USA), which have passive infrared sensors active during the day and infrared flash at night. In PR, we used Reconyx HC500 cameras (Reconyx Inc., Holmen, WI, USA) with infrared flash locked on day and night, which were previously used to identify melanistic Leopard in Malaysia (Hedges *et al.*, 2015). The use of IR allowed us to distinguish the individual markings on melanistic Leopard, thereby allowing for the first density estimates of Leopard in the study sites containing melanistic individuals. In SrWS and PPWS, where only spotted Leopard occurred, we used the Panthera V6 flash cameras (Panthera, New York, USA).

3.3.4 Analyses

3.3.4.1 Activity Patterns

We examined Leopard activity patterns and measured the overlap between the species and both its main prey (i.e., cervids and Wild Pig *Sus scrofa*), and anthropogenic factors, by using the method developed by Ridout and Linkie (2009) performed using the R package 'overlap' v.0.3.2 (Meredith and Ridout, 2018). Anthropogenic factors included records of illegal activities (e.g., logging, poaching), as well as records of domestic animals (i.e., dogs and cattle), which typically were accompanied by illegal intruders in our study areas. We excluded photographs of researchers and park staff, which, although they may have temporally caused disturbances, were not associated with major anthropogenic stressors. In addition, both sites in Malaysia had tourists who were accompanied by guides and restricted to certain tails. We excluded tourists from the anthropogenic factors because previous research showed that tourists did not affect diel activity patterns of mammals, including the Leopard, in Malaysian parks (Ota *et al.*, 2019), where there is typically less illegal human activity

compared to eastern continental Southeast Asia (i.e., Vietnam, Cambodia, Laos). To assess activity patterns, non-parametric circular kernel-density functions were used, where the observed capture times were regarded as random samples from underlying continuous distributions (Ridout and Linkie, 2009). In pairwise comparisons we determined the coefficient of overlapping (Δ), which ranged from 0 (no overlap) to 1 (complete overlap), between species activity patterns by measuring the area under the probability density functions. We used the nonparametric estimator of the coefficient of overlapping $\widehat{\Delta}_1$, and calculated 95% confidence intervals of each overlap index by generating 10,000 smoothed bootstrap samples (Meredith and Ridout, 2018), by first fitting a kernel density to the original data and then drawing random simulated observations from this distribution. To account for differences in latitude of the study areas, as well as the successive changes of the sun's position throughout the year in the celestial sphere (Nouvellet *et al.*, 2012), we determined sunrise and sunset times based on the dates and locations, and each record mapped sunrise and sunset to $\pi/2$ and $3\pi/2$, respectively. Leopard was classified as mostly diurnal (10–29% of records at night), mostly nocturnal (70–89% of records at night), or cathemeral (30–69% of records at night). We considered $\widehat{\Delta}1 \geq 0.70$ and $\widehat{\Delta}1 \leq 0.35$ as high and low overlap, respectively. In PR, the number of anthropogenic records was lower than the number of observations required to assess activity pattern; therefore, the coefficient of overlapping was not estimated for this site. All analyses were performed in R version 3.6.1 (R Core Team, 2019).

3.3.4.2 Density estimation

Leopard individuals were identified based on the unique spot patterns, and sex determined, when possible, based on the presence of distinctive morphological features (i.e., secondary sexual traits). Because dependent subadults (i.e., those photographed with their presumed mother) are not reliably photographed, these were removed from the analyses. For each detection, the same 2 researchers identified individual animals from the pelage markings. We considered a conservative approach when identifying individuals by excluding those who were not clearly identifiable by both image reviewers. We created a reference collection of both flanks, and for individuals with photos of only one flank, we used the side with the highest number of records to avoid double counting. We defined

24 hours as one sampling occasion, and considered a single detection per individual per station on each occasion. We treated the pair of cameras at each camera-trap location as one single station, which we considered operational if at least one camera was functional. When a station was not operational, we set the effort for that station and occasion to zero. We estimated the mean maximum distance moved and the Root Pooled Spatial Variance for each study area.

Density estimates were obtained using spatially explicit capture-recapture (SCR) models implemented within a Bayesian framework. By explicitly modelling the spatial organisation of individuals relative to the sampling devices, as well as considering the location of individual detections, SCR models account for imperfect detection and variation in detection among individuals due to differential overlap with the sampling devices. These models yield spatially-explicit estimates of abundance which can readily be translated into population density, representing a more robust advance over traditional, non-spatial approaches (Chandler and Royle, 2013, Royle *et al.*, 2014). In SCR models, detection is modelled as a decreasing function of distance between a given trap and the activity centre of an individual (Royle *et al.*, 2014). We used a half-normal detection function, which is defined by two parameters: the baseline encounter probability parameter (p_0) or probability of detecting an individual at the activity centre, and the spatial scale parameter (σ) that describes the decline in probability of detection with distance from the activity centre (Efford and Fewster, 2013, Royle *et al.*, 2014). Information on the location of individual activity centres comes from the spatially-explicit detection data, and density is estimated as the number of activity centres in the spatial domain of the model, or the state-space, divided by its area. The state-space was created by buffering each of the trapping grids by at least 4σ, using a discrete set of equally spaced points, representing potential Leopard activity centres (Royle *et al.*, 2009a, Royle *et al.*, 2009b). Because the Leopard is a habitat generalist and the core areas where the surveys were conducted were mostly surrounded by forested areas, we considered the buffer area as suitable habitat, and only excluded regions from the state-space that were distinctly non-habitat (e.g., oceans, large lakes). The 3-month survey period should provide sufficient data for the Leopard which typically has low-detection probability, whilst minimising the likelihood of activity centres changing considerably and ensuring demographic closure. Despite the practical benefits of likelihood-based inferences (e.g., model

selection by AIC), we used a Bayesian framework given the sparsity of the data. Bayesian inference does not rely on asymptotic arguments and is valid irrespective of sample size (Royle *et al.*, 2009a), and available programs allow for flexibility to include additional model specifications, such as the inclusion of model random effects.

Leopard densities were estimated by subspecies. However, because data for the Indochinese Leopard were too sparse to reliably estimate model parameters separately for each site, we constructed combined SCR models with shared parameters as this strategy has been shown to increase precision in SCR-based density estimates (Wilting *et al.*, 2012). Specifically, we constructed combined SCR models with shared parameters across surveys within groups classified as northern (Cambodia, Thailand) and southern (Malaysia) sites, to represent differences in climate, habitat and cultural beliefs, which have been shown to affect prey populations and trophic niches of Leopard (Ghoddousi *et al.*, 2017). The northern sites (SrWS, PPWS, SaWS), all north of the Isthmus of Kra, are characterised by more open forests and pronounced dry seasons. In contrast, the southern sites (TNNP, PR), all south of the Isthmus of Kra, are characterised by closed evergreen forests that have considerably higher annual rainfall and less pronounced dry seasons. In addition, because previous research showed that local religion can have an important effect on the prey species targeted by poachers, which in turn can affect the prey base of the Leopard (Ghoddousi *et al.*, 2017), the grouping also considered religious differences among sites, with northern sites being within predominantly Buddhist countries, and southern sites within a predominantly Muslim country.

We assumed either the movement-related parameter, σ, or the baseline encounter probability parameter, p_0, was constant across sites (i.e., σ or p_0 was estimated from data generated across sites within a group), but allowed each study area to have a separate density estimate. This approach reflects the assumption that ecological circumstances were comparable, with individuals in the grouped study areas having similar-sized home ranges, or baseline detection probabilities. We considered this to be plausible because the habitats from the pooled study areas were similar and surveys were conducted during the respective dry seasons and with largely standardized survey protocols, suggesting that Leopard should have similar area requirements or detection rates.

Accounting for differences in movement and detection probability between sexes improves density estimates in felid species where males and females have different home range sizes and movement patterns (Sollmann *et al.*, 2011). Therefore, we modelled sex-specific detection parameters for the Indochinese Leopard surveys, allowing for different sex ratios across study areas (hereafter full models). Modelling sex-specific parameters was not possible for the Javan Leopard because of the low number of males detected. Although the models could conceivably extend to arbitrary levels of complexity, by considering individual heterogeneity or time effects (e.g., temporal variation in detectability), the complexity of the models was limited due to the sparsity of the data, and to avoid poorly identifiable models (Dorazio and Royle, 2003) or extreme sensitivity to model choice. In addition to the sex-specific models, we ran null models to allow for comparisons between areas and with previous studies, as different model structure can induce different parameter estimates. Because sex differences are not accounted for in the null models, which may translate into bias in overall density estimates, null model densities resemble an index to density.

We used the information on Leopard movements from the models to estimate an approximate home range size. Under a half-normal detection model, the encounter probability is proportional to the kernel of a bivariate normal (Gaussian) probability density function, which allows the conversion of the movement parameter σ to the radius of a bivariate normal model of space usage. Consequently, we used the estimated σ to compute 95% use areas (i.e., areas which contains 95% of the movement outcomes) according to:

$$A_{.95} = \pi \left(\sigma \sqrt{5 \cdot 99}\right)^2$$

where 5.99 is the value of a chi-square distribution with an alpha (α) critical value of 0.05 on 2 degrees of freedom, arising from movement being represented by a bivariate normal distribution (Royle *et al.*, 2014).

To date, few studies have suggested how to evaluate the fit of SCR models, particularly when using Bayesian analysis (Royle *et al.*, 2014). Following the approach suggested by Royle *et al.* (2014), we constructed fit statistics based on aggregated observed (y) and expected (E) frequencies.

Specifically, we evaluated the goodness-of-fit of the models by conducting a Bayesian *p*-value analysis of the observation component of the models using 3 fit statistics from Freeman-Tukey residuals:

Fit Statistic 1 – individual and trap-specific counts aggregated over all sample occasions

$$T1(\mathbf{y}, \boldsymbol{\theta}) = \sum_i \sum_j (\sqrt{y_{ij.}} - \sqrt{E(y_{ij.})})^2$$

Fit Statistic 2 – individual encounter frequencies, aggregating for each individual

$$T2(\mathbf{y}, \boldsymbol{\theta}) = \sum_i (\sqrt{y_{i..}} - \sqrt{E(y_{i..})})^2$$

Fit Statistic 3 – trap frequencies, aggregating over individuals and replicates

$$T3(\boldsymbol{y}, \boldsymbol{\theta}) = \sum_j (\sqrt{y_{.j.}} - \sqrt{E(y_{.j.})})^2$$

where θ represents all parameters in the model. We obtained Freeman-Tukey discrepancies between the expected number of detections and both the observed detections and simulated number of detections, based on values of the parameters at each Markov Chain Monte Carlo (MCMC) iteration. Posterior predictive checks of the models suggested heterogeneity among traps, therefore we extended the models to include a trap-level random effect for probability of detection. We generated density and individual activity centre maps using posterior distributions.

3.3.4.3 Habitat Use

We assessed Leopard habitat use by adopting a hierarchical formulation of the single-species single-season occupancy model. We defined each station as a site and collapsed photographic data into a binary format for 15-day occasions, to reduce overdispersion and increase temporal independence of detections. Given that likely there were multiple cameras within each Leopard's home range, habitat use (i.e., the probability that any one site was used by Leopard) during the study period, rather than true occupancy, was modelled. We identified covariates by screening different environmental and anthropogenic covariates at different scales (Appendix 3.1), then implemented a final model in a Bayesian framework. We selected site covariates based on *a priori* knowledge and previous studies

on Leopard. Because ecological processes and patterns are scale-dependent, reliable predictions of wildlife habitat associations are dependent on an adequate definition of the spatial scale of the covariates that are relevant to the study species (Mayor *et al.*, 2009). To identify the optimal scale for predictor variables, we used a scale-optimisation (see Appendix 3.1). The different radii distances considered (i.e., 0.3, 1, 2, 4, 8, 15, and 30 km) for scale optimisation were selected to represent the ecological responses of Leopard across scales relevant to meet its daily requirements, from resources within habitat patches, to reported distances travelled daily during dry season (29 km^2; Hubel *et al.*, 2018), and considering the movement parameter of the species in the different habitats, derived from the density section of this study. Prior to modelling, all covariates were standardized to a zero mean and unit standard deviation, and their collinearity was tested using Pearson's correlation, considering pair-wise combinations with a correlation coefficient $r \geq 0.7$ as strongly correlated (Dormann *et al.*, 2013).

We ran a combined Bayesian occupancy analysis for all study areas. Large-scale studies are likely to incur sampling inequities due to ecological and geographical idiosyncrasies, as well as local constraints on survey implementation, arising from differences in funding, time, or available resources. Consequently, to account for the known sampling inequities, and the unobserved heterogeneity across space and time, we used area level random effects. This hierarchical occupancy model approach allows for more robust inferences in the study areas where data were sparse by borrowing strength from areas where more data were collected. We modelled site use probability as a function of 6 predictor variables and an area-level random effect. Specifically, we modelled the effect on site use of 6 covariates representing both anthropogenic and environmental factors: distance to water sources (8 km-radius focal mean), elevation (8 km-radius focal mean), forest loss (15 km-radius focal mean), normalized difference vegetation index (NDVI, 1 km-radius focal mean), detection frequencies of anthropogenic factors (i.e., illegal human activities, domestic animals), and detection frequencies of presumed preferred prey species (Appendix 3.1). We classified all photographs of primates, small to medium ungulates, and small carnivores as preferred prey based on previous dietary studies of Leopard conducted in the region (Grassman, 1999, Rabinowitz, 1989, Rostro-García *et al.*, 2018, Steinmetz *et al.*, 2013) and on previous results showing that Leopard

preferentially prey on species within a weight range of 10-40 kg (Hayward *et al.*, 2006; see Appendix 3.1 for more details). The habitat use probability at each site *i* was modelled as a function of site covariates such that:

$$\text{logit}(\psi_i) = \beta_0 + \beta_1\text{DistWat}_i + \beta_2\text{Elev}_i + \beta_3\text{ForLoss}_i + \beta_4\text{IAnthr}_i + \beta_5\text{NDVI}_i + \beta_6\text{PPrey}_i + \varepsilon_{\text{Area } i}$$

where β_0 is the intercept, $\beta_{1\text{-}6}$ are the regression coefficients of the evaluated covariates, and $\varepsilon_{Area\ i} \sim Normal(0, \tau)$ is the area-level random effect. This formulation assumes that patterns in habitat use were comparable across the study areas, which we considered plausible given that our surveys were conducted during the respective dry seasons.

Detection probability had an area-level random effect, to allow for differences in baseline detection among study areas, which for example could arise from differences in behaviour or in abundance. We further modelled detection probability as a function of camera placement (i.e., on or off road), a factor shown to influence detection in big cats (Sollmann *et al.*, 2011), and differences in effort. We accounted for varying effort that resulted from camera malfunctioning, fire, or disturbance by animal or human, by including the number of days each station was functional within a 15-day occasion as a covariate on detection. The detection probability for survey *j* at location *i* then was modelled as:

$$\text{logit}(p_i) = \alpha_0 + \alpha_1\text{Road}_i + \alpha_2\text{Eff}_{i,j} + \varepsilon_{\text{Area } i}$$

where α_0 is the intercept, α_1 and α_2 the effects of camera-trap placement and effort on detection probability, respectively, and $\varepsilon_{Area\ i} \sim Normal(0, \tau_p)$ the area-level random effect. To further evaluate differences among Indochinese Leopard study areas, we grouped sites into northern (Cambodia, Thailand) and southern (Malaysia) sites, and ran two additional models considering the same covariates. The data were too sparse to reliably estimate Javan Leopard habitat use separately for MBNP. We considered a coefficient to have a strong support if the 90% Bayesian credible intervals (BCI) did not overlap zero, and moderate support if the 75% BCI did not overlap zero.

We calculated a Bayesian *p*-value to test if the habitat use model adequately fit the data (Gelman *et al.*, 1996), with values close to 0.5 indicating model fit. We obtained this value by calculating a fit statistic (i.e., residual) that depended on the model parameters and the observed data,

obtaining the same fit statistic for a simulated set of data generated from the model under consideration, and then calculating the proportion of times the residuals from the newly generated data were smaller or larger than those from the original data. We used Freeman-Tukey residuals, *R*, such that:

$$R(\mathbf{y}, \boldsymbol{\theta}) = \sum (\sqrt{y} - \sqrt{E(y)})^2$$

where *y* are the detection frequencies (i.e., binary data aggregated across occasions), θ represents all parameters in the habitat use model, and *E(y)* is the expected value of *y*.

3.3.4.4 Spatial autocorrelation

Occupancy models assume independence of sampling locations, which can be violated when camera-trap locations are spaced too closely together, resulting in single individuals occurring at several sampling locations. Because Leopard home range diameter likely exceeded the average camera-trap spacing, we suspected autocorrelation between adjacent camera-trap stations. Therefore, to test for spatial autocorrelation in response variables not accounted for by predictor variables we calculated Moran's I for residuals from the habitat use model, following the approach suggested by Moore and Swihart (2005). We calculated residuals as whether or not Leopard was detected at all at site *j* (non-detection = 0, detection = 1), minus the predicted probabilities of detecting Leopard at least once, given as:

$$\psi_j * p.tot_i$$

where ψ_j is the habitat use probability of Leopard at site *j*, and

$$p.tot_i = 1 - \prod_{k=1}^{K} 1 - p_{jk}$$

where p_{jk} is the detection probability of Leopard at site *j* and occasion *k*.

We calculated Moran's I across different neighbourhood distances, which represented multiples of the average trap spacing of the different study areas, using model-averaged estimates and binary distance weight. To avoid possible violations of the normality assumption, given that

residuals were constrained between -1 and 1, and to determine whether spatial autocorrelation was significant, we bootstrapped Moran's I using Monte-Carlo simulations.

3.3.4.5 Model implementation

We implemented all SCR and occupancy models in a Bayesian framework using JAGS (Plummer, 2003), accessed through R ver. 3.6.1 (R Core Team, 2019) using the R package jagsUI ver. 1.5.1 (Kellner, 2019). We ran three parallel Markov chains with 400,000 iterations each, of which we discarded 50,000 as burn-in, and we thinned the remaining iterations by 20 to make the output more manageable. For the sex-specific SCR models, due to memory limitations, we ran three parallel Markov chains with 200,000 iterations each. For each parameter we assessed chain convergence using the Gelman-Rubin statistic, assuming that values $\hat{R} < 1.1$ indicated convergence (Gelman *et al.*, 2004), and visually inspected the trace plots. We report the results as posterior mean and standard deviation, and 95% (i.e., the 2.5^{th} and 97.5^{th} percentiles of the posterior distribution) BCI.

3.4 Results

The camera-trap surveys conducted in 7 study areas across 4 countries yielded a total of 189 Leopard capture events during 24,684 camera trap nights at 314 camera-trap stations (Table 3.1). We did not detect Leopard in KSWS; thus, this area was not considered in subsequent analyses. There was a difference in success rate of identifying individual Leopard from the photographs based on: 1) whether Leopard was spotted or melanistic, and 2) the camera model used. For example, in TNNP, where we recorded only melanistic Leopards, a total of 17 detections (27.0% of all detections) of Leopard could not be used to identify individuals because spot patterns were not visible, despite the use of the Panthera V6 IR cameras. In contrast, all melanistic Leopard records from PR could be identified to individual because the spot patterns were always visible in the photographs taken with Reconyx HC500. In most cases when Leopard identification was not possible from Panthera V6 IR camera photos, it was due to inadequate exposure caused by background lighting and distance of the

Leopard from the camera. All records of non-melanistic Leopard could be identified to individuals by all camera models.

3.4.1 Activity Patterns

The activity patterns of Leopard differed considerably among study areas, ranging from 12.5% to 90.0% of records occurring during daylight (Table 3.2). In Malaysia and Indonesia, Leopard was mostly diurnal, whereas in Cambodia and Thailand, Leopard was mostly nocturnal or cathemeral (Table 3.2). The frequency of records of anthropogenic factors was highest in Cambodia, and lowest in Malaysia. Leopard activity overlapped most strongly with anthropogenic factors in MBNP ($\hat{\Delta}_1$ = 0.77), and considerably less so in SrWS ($\hat{\Delta}_1$ = 0.34; Table 3.2), where the number of anthropogenic records was the highest (37.6 times larger than that of MBNP). Leopard activity overlapped most strongly with cervids ($\hat{\Delta}_1$ = 0.82) and Wild Pig ($\hat{\Delta}_1$ = 0.81) in SaWS and the least with cervids in SrWS ($\hat{\Delta}_1$ = 0.61) and Wild Pig in PPWS ($\hat{\Delta}_1$ = 0.69; Table 3.2; Figure 3.3 and Figure 3.4).

3.4.2 Density Estimates

A total of 36 adults (18 spotted and 18 melanistic individuals) were identified across sites, of which 24 were females (66.7%), 11 males (30.6%), and 1 of unknown sex (2.8%). Given that some individuals were captured more than once by the same camera trap within a 24-hour period, a total of 161 capture events were used in subsequent analyses. Individuals were captured between 1 and 20 times, with a mean of 4.5 captures per individual. Although more individual females than males were detected in the study areas, particularly in PPWS where only females were detected, males were detected more frequently than females (average female detection frequency = 3.3, average male detection frequency = 7.3). The mean maximum distance moved (MMDM ± SE) ranged from 2.9 ± 0.8 km to 13.7 ± 1.9 km across sites, and was 2.6 times larger for males than females. The average Root Pooled Spatial Variance was 2.3 km.

The estimated Leopard densities varied considerably across study areas. Under the null model, ran for consistent among-area comparisons, density estimates (± SD) at the 6 sites ranged

from 0.23 ± 0.11 to 4.74 ± 1.72 Leopard/100 km^2 (Table 3.3). The Javan Leopard had the highest density estimate (4.74 ± 1.72 Leopard/100 km^2), almost twice as high as the highest density estimate of Indochinese Leopard (2.63 ± 0.86 Leopard/100 km^2). The density of the Indochinese Leopard under the null model varied 10-fold, from the lowest in SaWS (0.23 ± 0.11 Leopard/100 km^2) to the highest in TNNP (2.63 ± 0.86 Leopard/100 km^2). In addition, when comparing null models, the movement parameter sigma (σ) was significantly larger in the northern countries (Cambodia, Thailand) than in the southern countries (Malaysia and Indonesia), and larger for the Indochinese Leopard compared to the Javan Leopard. Consequently, the estimated home range size was largest for Indochinese Leopard inhabiting the more open forests of the northern countries (Mean ± SD: 320 ± 69 km^2), almost 6 times larger than that of the Javan Leopard (56 ± 28 km^2). Baseline encounter probability p_0 was highest for the Javan Leopard and lowest for the Indochinese Leopard inhabiting northern countries (0.015 ± 0.005 and 0.010 ± 0.002, respectively) although 95% BCI overlapped.

The posterior checks of the full models extended to include a random effect for probability of detection indicated good fit to the data. Overall, these full models produced density estimates similar to those of the null models, except for surveys conducted in Malaysia in which the estimated density was larger than under the null model (Table 3.3). In addition, the full models suggested larger σ for males than females irrespective of the area, indicating males had larger home ranges than females across sites. The density maps showed clear spatial variation for the different areas, revealing a heterogeneous distribution of Leopard across the study sites, with specific Leopard density hotspots (i.e., areas within the state-space with a concentration of high-density pixels). These hotspots were located in more remote areas or in close proximity to ranger stations or park headquarters, except in PR where the highest density pixels were located in the eastern edge of the trapping array, which was closer to villages.

3.4.3 Habitat Use

When considering the 6 study areas in which Leopard was detected, we obtained data from 270 stations totalling 21,087 trap nights, in which over 40 mammal species >1 kg were detected. We identified all mammals to species, with the exception of those in which the quality of the picture did

not allow to discern to species level, in which case we used the genus as the classifying units. The community of species varied in number and composition per study site, with over a twofold difference between the number of species detected in the most (i.e., TNNP) and least (i.e., MBNP) diverse areas. Similarly, the proportion of sites at which Leopard was detected varied considerably among study areas, with over a twofold difference between the area with the most (TNNP: 38.3% of stations) and fewest (PR: 16.7% of stations) sites with Leopard detections (Table 3.1).

We retained all top-performing covariates at their best-performing spatial scale (Appendix 3.1) as no pair-wise combination showed significant collinearity (i.e., all correlation coefficient $r < 0.7$). The Gelman-Rubin diagnostic indicated adequate convergence of all parameters, and the Bayesian *p*-values suggested that the model adequately described the data. The probability of Leopard detection increased with effort and decreased when traps were located on roads (Table 3.4). Leopard used sites with lower elevation (measured at an 8-km scale), and with higher NDVI (1-km scale), with the former more strongly associated with habitat use by the species (Table 3.4, Figure 3.5). In addition, Leopard habitat use had a positive association with forest loss (15-km scale), although the study areas had low (<8%) occurrence of forest loss, and the 75% BCI of the coefficient encompassed zero. There was a negative association with distance to water, humans, and preferred prey, although the effects were weak with 75% BCI's encompassing zero (Table 3.4, Figure 3.5, Figure 3.6). The mean detection probability was 0.265 (SD = 0.097) and the mean posterior habitat use probability was 0.341 (SD = 0.180), with 25-45% of sites estimated to be used by Leopard in the different areas. Only one study area (TNNP) showed significant spatial autocorrelation in model residuals at the smallest neighbourhood distance tested (Table 3.5). We acknowledge that for TNNP we may have underestimated habitat use; however, the value of the statistic was low (MI = 0.222). Thus, due to the sparsity of the data and that we were interested in the probability of any one site being used by Leopard instead of true occupancy, we decided not to add a spatial component to the model to avoid poorly identifiable models. In all but the aforementioned case, Moran's I statistic was <0.1, indicating low levels of spatial autocorrelation in model residuals (Table 3.5).

The evaluation of the northern and southern Indochinese Leopard sites revealed additional region-specific responses in habitat use covariates. In the northern sites, NDVI had a strong positive

effect on Leopard habitat use, whereas presumed preferred prey had a moderate negative effect. In addition, we found a weak negative effect of forest loss on Leopard habitat use, with around 70% of the posterior probability mass being negative, although the 75% BCI encompassed zero. In contrast, Leopard habitat use in the southern sites had a strong positive association with presumed preferred prey, a moderate positive association with both forest loss and anthropogenic factors, and a moderate negative association with distance to water. Leopard detection probability increased when stations were located on roads in the southern sites, whereas road placement had a moderate negative effect on Leopard detection in the northern sites.

3.5 Discussion

We provide the first density estimates of Leopard in 5 study areas that represent some of the last remaining viable populations of the Critically Endangered Indochinese and Javan Leopard in Southeast Asia. Our density estimates are among the lowest ever reported for Leopard in Asia, and indeed within the species' worldwide distribution (Table 3.6), suggesting the Leopard in Southeast Asia is at risk of extirpation. Previous studies using SCR models showed Leopard densities throughout the world typically were 3-7 Leopard/100 km^2 (mean density from 35 different areas was 5.81 Leopard/100 km^2; range: 0.62-14.7 Leopard/100 km^2; Table 3.6) including in unprotected, human-dominated landscapes (Athreya *et al.*, 2013). In contrast, Indochinese Leopard densities estimated in this study were all below 3 Leopard/100 km^2. In particular, the Leopard densities in SaWS in Thailand (0.23 Leopard/100 km^2) and SrWS in Cambodia (0.56 Leopard/100 km^2) were the lowest density estimates ever reported for the species, and were comparable only to that of a population of the Critically Endangered Amur Leopard in China (0.62 Leopard/100 km^2; Qi *et al.*, 2015). Even in MBNP in Java, where we found the highest Leopard density among our surveys, it was still less than half the density previously reported for Javan Leopard in the western edge of the island (Rahman *et al.*, 2018).

The low Leopard densities in Southeast Asia likely are related to the pervasive snaring crisis that is causing wildlife extinctions throughout the region and impacting over 700 mammal species (Belecky and Gray, 2020). The Leopard populations in Cambodia and Thailand had the lowest

densities and seemed to be particularly under threat, suggesting high extinction risk, at least in our study areas. Unexpectedly, no Leopard was detected in KSWS in southern Thailand, despite being an area with sufficient habitat and prey numbers. Leopard was last recorded in KSWS in 2014 (Rostro-García *et al.*, 2016a), but it was not detected in our study or a concurrent camera-trapping study (Petersen *et al.*, 2020), suggesting the species is now likely to be functionally extinct in, if not fully extirpated from, the entire Khlong Saeng-Khao Sok protected-area complex (Rostro-García *et al.*, 2019). The lowest density estimated in our study occurred in SaWS, which may have been a function of the larger survey area that included portions outside of the core zone that supported fewer individuals. Nonetheless, the SaWS is part of WEFCOM, the largest protected-area complex in Thailand where Leopard still occurs (Rostro-García *et al.*, 2019), thus we expected a higher density. Leopard and other wildlife in SaWS likely have been negatively affected by the rapid economic development of the area. The growing human population, increased agricultural activity, as well as the construction of roads and building of the Srinakarin and Thathungna dams, have contributed to habitat fragmentation in and around SaWS, affecting populations of large mammals (Chaiyarat *et al.*, 2015, Van de Water and Matteson, 2018). In addition, poaching, logging, bamboo cutting, cattle-grazing, collection of non-timber forest products, and fires exacerbate the anthropogenic pressures in the area (Stewart-Cox, 2012). Given the limited size of undisturbed areas in SaWS, conservation efforts should focus not only on restoring and maintaining available habitat and animal populations, but also on securing corridors that allow wildlife to move to and from adjacent protected areas. Because SaWS seems to have sufficient habitat and prey base, likely it is possible for the Leopard population to recover with immigrants from nearby protected areas, particularly Huai Kha Khaeng Wildlife Sanctuary, the most intensively patrolled park in Thailand (Duangchantrasiri *et al.*, 2016) that appears to have a relatively healthy Leopard population (Simcharoen *et al.*, 2008).

In Cambodia, the Leopard density estimate obtained for SrWS showed a steep decline of about 50% in 2 years (Rostro-García *et al.*, 2018) and over 80% decline from 2009 (Gray and Prum, 2012). Although we expected a decline in Leopard density in SrWS, due to recent increases of poaching in the region (Gray *et al.*, 2017) and a previously reported Leopard population decline (Rostro-García *et al.*, 2018), such an sharp decline over 2 years was not expected. Moreover, despite

sampling the same area of the core zone, the individuals captured were all different from those captured 2 years prior to this study (Rostro-García *et al.*, 2018) indicating a complete turnover of the population in 2 years. This is one of the largest density decreases ever documented in a Leopard population and suggests the Leopard population in SrWS faces imminent extirpation. Surprisingly, Leopard density in SrWS was lower than the adjacent PPWS, despite the latter being a smaller protected area with villages inside the park. In addition, based on line-transect surveys conducted in both parks (WWF Cambodia, unpubl. data), the density of the Leopard's preferred prey, Muntjac (*Muntiacus vaginalis*), was similar between SrWS and PPWS, indicating that differences in preferred prey densities likely were not responsible for the differences in Leopard density between sites. Higher levels of poaching, and in particular snaring, likely were responsible for the dramatic decline in Leopard density in SrWS compared to PPWS. Indiscriminate widespread snaring, mostly targeting common species (e.g., Wild Pig and Muntjac) for the illegal bushmeat market, has been increasing in the landscape (Gray *et al.*, 2017, Rostro-García *et al.*, 2018). The SrWS shares a border with Vietnam, which results in an influx of poachers from across the border to supply the high demand of wildlife products, particularly bushmeat (Shairp *et al.*, 2016). Vietnam, which has been identified as a significant consumer of wildlife, also exports to foreign urban markets in countries such as China and Korea, and thus is considered a key distribution centre of wildlife (Sandalj *et al.*, 2016). Although further from the Vietnamese border than SrWS, PPWS is not protected from poaching pressures, indicated by the more than 7,000 snares removed from PPWS over a 4-year (2015-2019) period (Belecky and Gray, 2020). Increases in snaring possibly explain why no male Leopard was detected in PPWS, as males are more prone to being killed than females due to their larger home ranges, which increases their chances of being snared and often brings them closer to park boundaries where human threats are higher. The heterogeneous distribution of Leopard observed in Cambodia suggested not only avoidance of more disturbed areas within the parks, but also is characteristic of defaunated landscapes, where species often show extreme spatial heterogeneity because extirpations result in reduced, often patchy, distributions (Tilker *et al.*, 2020).

Leopard densities in Malaysia were higher than those obtained for Cambodia and Thailand, particularly in TNNP, where we obtained the highest density estimate for the Indochinese Leopard.

This likely was due to the vastness and remoteness of TNNP, which has one of the lowest road densities in the world (0.023 km/100 km^2; Kawanishi and Sunquist, 2004) and a lower level of human impact compared to other sites. Despite the sparsity of Leopard data, the PR, adjacent to the TNNP, had the second highest density estimated for the subspecies, demonstrating this logging concession has the capacity to act as an extension or buffer zone of TNNP. Nevertheless, these density estimates are still lower than those reported for several areas within the species' global distribution (Table 3.6). Tropical rainforests do not support the diversity or abundance of large terrestrial ungulates some other ecosystems can support (e.g., savannahs; Kawanishi and Sunquist, 2004). The lower on-the-ground productivity, a consequence of the lush canopy that characterises this habitat, results in reduced ungulate biomass, which in turn supports lower densities of large carnivores (Rayan and Linkie, 2016). Therefore, it is not surprising that estimated Leopard densities in the rainforests of Malaysia were relatively low compared to other sites in Asia and Africa. Although we were unable to evaluate the impacts of and co-benefits from the specific forestry practices implemented in PR given the lack of baseline data, our results illustrate the potential of selectively logged forest to support Leopard populations, similar to that found for Tiger populations in the country (Rayan and Mohamad, 2009). In addition, we recorded an overall mammalian diversity similar to that of TNNP, which indicates that PR retained the expected biodiversity, including some of Peninsular Malaysia's most Threatened species (Clements *et al.*, 2021). Nonetheless, akin to that found for the Tiger (Rayan and Linkie, 2015), Leopard density in TNNP was almost three times higher than that of PR, emphasising the need for better wildlife management within forest reserves. Additional systematic evaluations of the status of the species and the contributions that certified forests have on wildlife conservation are required to reduce forestry practices that decrease biodiversity, and to identify specific restoration or enforcement actions, particularly in areas such as PR which currently lack active enforcement. Weak or non-existent wildlife protection measures make forest reserves more vulnerable to illegal activities, which in Peninsular Malaysia are mostly undertaken by foreign encroachers from neighbouring countries. This has been highlighted as a possible threat to the Tiger in TNNP, and other forests throughout Malaysia (Kawanishi and Sunquist, 2004), and the same likely is true for the Leopard.

The MBNP has been identified as one of the few areas in the drier forest of eastern Java to support Leopard and one of only three national parks identified on the island to potentially support more than 50 individuals (Wibisono *et al.*, 2018). Therefore, it was unexpected that the Leopard density in MBNP was less than half of that found in western Java (Rahman *et al.*, 2018). Reasons for this large density difference are unknown, although we suspect the higher precipitation and thus plant productivity of western Java might have resulted in a greater biomass of potential prey compared to East Java, allowing for a larger Leopard population to be sustained. Of all Leopard subspecies, the Javan Leopard has the highest human density in its extant range, which restricts the availability of suitable habitat to less than 9% of the island (Wibisono *et al.*, 2018). Nevertheless, compared to our mainland sites, Leopard in MBNP had a relatively high density while occurring within a site with the lowest mammalian diversity. This exemplifies the behavioural plasticity of the Leopard, which allows this species to persist in relatively small protected areas surrounded by human development and high human densities, similar to that found for some populations of Leopard in India (Athreya *et al.*, 2013, Kumbhojkar *et al.*, 2020).

Overall, Leopard habitat use was influenced most strongly by topography and vegetation productivity. Specifically, Leopard preferred areas at lower elevation at a broader scale and higher NDVI at a finer scale. The importance of lower elevations on Leopard habitat use could be driven by the prey availability, which occur mostly in low elevation areas (Ratnayeke *et al.*, 2018, Rayan and Linkie, 2015). Although higher elevation areas likely are more difficult to access, thus serving as a measure of remoteness within most landscapes (Mann *et al.*, 2020, Tilker *et al.*, 2020), higher elevation areas also are linked to certain ecological attributes, including microclimate and forest structure, that might not benefit prey and consequently Leopard. The NDVI, which directly correlates with photosynthetically active biomass or vegetation productivity, can be used as a good proxy of forage availability (Gavashelishvili and Lukarevskiy, 2008, Pettorelli, 2015) and thus likely represents preferred forage areas by Leopard prey. Moreover, the Leopard is a predator that hunts by stalking and ambushing prey (Balme *et al.*, 2007), therefore habitat use may have been driven by prey catchability, which likely was higher in areas with more vegetation cover, as group sizes of prey species and their ability to detect predators are lower compared to more open habitats (Rostro-García

et al., 2015). In addition, the Leopard may have selected for dense habitats not only because of the increase in prey susceptibility, and thus hunting success, but also to reduce potential risks (e.g., being detected by larger predators, such as Tiger, or humans). Our findings were consistent with previous studies conducted in the region which reported that large carnivores, including Leopard, preferred areas with lower elevation and higher NDVI (Gavashelishvili and Lukarevskiy, 2008, Rahman *et al.*, 2018, Ratnayeke *et al.*, 2018, Rayan and Linkie, 2015, Wang *et al.*, 2018).

There were noteworthy differences in Leopard habitat use among the Indochinese Leopard study areas which likely were linked to differences in habitat and human culture. Specifically, in the northern sites which are characterised by more open habitats, NDVI had a strong positive effect on Leopard habitat use, whereas in the tropical rainforest of the southern sites, where NDVI was consistently higher, it had a weak effect. The camera-trap surveys were carried out during the dry season when monthly temperatures are the highest particularly in the northern sites. In the case of the Cambodian study areas, the grassy understory burns during the dry season, which may have caused the Leopard to favour sites with more vegetation to improve hunting success and provide shelter from high temperatures and fire. Also, in the northern sites the Leopard avoided areas with less vegetation, and presumably cover, possibly to evade humans, which were more prevalent in the landscape compared to the southern sites. In addition, in the northern sites the presumed preferred prey had a moderate negative effect on Leopard habitat use, which was unexpected given that prey abundance often determines the spatial distribution of apex carnivores (Fuller and Sievert, 2001, Karanth *et al.*, 2004, Rich *et al.*, 2017). This result likely was influenced by wildlife market preferences and greater human pressure, particularly poaching, in the northern sites, where the most common species (i.e., Wild Pig and Muntjac) were both the most sought-after species of the bushmeat trade (McEvoy *et al.*, 2019, Sandalj *et al.*, 2016, Shairp *et al.*, 2016) and the preferred prey of Leopard (Rostro-García *et al.*, 2018).

Contrary to this, in the southern sites, where human disturbances and presumably poaching were considerably lower, habitat use patterns were typical for the species, with Leopard preferring areas with more preferred prey and closer to water sources. Unexpectedly, in the southern sites Leopard habitat use had a moderate positive association with both anthropogenic factors and forest

loss at a broad scale (i.e., 15 km). Although these study areas had low (<8%) occurrence of forest loss and lower numbers of anthropogenic records, our findings suggest that it is not human presence per se in a landscape that influences Leopard populations, but rather the type (e.g., logging vs. poaching) and intensity of the illegal activities. While we used detection frequencies of anthropogenic factors as proxies for illegal human activities, direct measures of the pressures imposed by these activities are difficult to obtain, not only because poaching is a cryptic phenomenon but also due to the low detectability of the methods used for poaching, particularly snaring (Dobbins *et al.*, 2020, O'Kelly *et al.*, 2018). The effect of humans on Leopard habitat use can be especially challenging to quantify in areas where humans are essentially omnipresent, such as at the Cambodian study areas. For that reason, in the northern sites, forest loss, which had a negative association with Leopard habitat use, likely served as a more direct measure of human impact, compared to anthropogenic factors which had a weak effect on Leopard habitat use. The negative influence of human activities in northern sites may explain why, contrary to the southern sites and previous studies on big cats (Sollmann *et al.*, 2011), roads had a moderate negative effect on Leopard detection, as these are heavily used by illegal encroachers in the northern sites.

Although, Leopard may have avoided humans at finer spatial scales not investigated in this study, such as the level of feeding or resting sites (Broekhuis *et al.*, 2013, Mateo Sánchez *et al.*, 2013, Rostro-García *et al.*, 2015, Rostro-García *et al.*, 2016b), our findings suggest Leopard and its main prey adjusted their temporal activity patterns to avoid humans in the northern sites. This was particularly evident in SrWS, which had the largest number of records of anthropogenic factors, and lowest temporal overlap between anthropogenic factors and Leopard. Previous studies have revealed a strong effect of humans on daily patterns of mammals, including Leopard, other big cats, deer and Wild Pig, who increased their nocturnality to avoid humans (Gaynor *et al.*, 2018, Ngoprasert *et al.*, 2017, van Doormaal *et al.*, 2015), with both direct and indirect effects of human activity linked to significant effects on their activity patterns (Ohashi *et al.*, 2013). In our study areas, this pattern was particularly obvious for Leopard and Wild Pig which were nocturnal in the northern sites, where there were high levels of human activities during daylight hours. Although an increase in nocturnality among wildlife in these areas demonstrates the high degree of behavioural plasticity of the species,

this shift in activity patterns can have negative and far-reaching ecological consequences. The cumulative effect of anthropogenic disturbances on the temporal dynamics can result in individual, population, community, or ecosystem-level consequences, by affecting fitness, evolution, population persistence and community interactions (Gaynor *et al.*, 2018, Ngoprasert *et al.*, 2017). Additional research is required to further evaluate the effects of temporal displacement on Leopard and prey populations.

In contrast to the northern sites, Leopard and its presumed main prey, notably Wild Pig, were primarily diurnal in our study areas in Malaysia and Java. Both sites in Malaysia had the lowest detection frequency of anthropogenic factors of our study areas, whereas MBNP in Java had the third highest detection frequency of anthropogenic factors, suggesting that human presence alone was not responsible for the differences observed in the activity patterns. There were important differences in the type and intensity of human activities between the northern and southern sites, which in turn appeared to be related to the religious beliefs, geographical location, and socio-economic levels of the countries in which the study areas were located. Malaysia and Indonesia are Muslim-majority countries, and due to the prohibition of Wild Pig consumption by Islam, the species is not consumed by most nationals of these countries (Kawanishi and Sunquist, 2004). The lower poaching pressure might result in a greater availability of Wild Pig, particularly in the park edges (Kawanishi and Sunquist, 2004) and near villages where the species can feed on crops and scavenge on garbage. This may explain why both Leopard and Tiger were detected in the eastern area of PR, close to nearby villages, rather than in the centre or western area of the reserve which was adjacent to the TNNP. In Iran, another Muslim-majority country, Wild Pig has experienced low poaching pressures due to religious beliefs, which led to higher densities inside protected areas and ultimately high consumption of this species by Leopard (Ghoddousi *et al.*, 2017). Contrary to this, in Vietnam, Wild Pig is the most commonly consumed bushmeat species (Sandalj *et al.*, 2016), and the same is likely true for neighbouring countries such as Cambodia and Thailand, where Wild Pig consumption is not a taboo. Accordingly, local poachers we interviewed in eastern Cambodia stated that Wild Pig was the main target of their snaring efforts. Consequently, >3,700 snares, set primarily for Wild Pig, were removed from SrWS during the year of our survey, which likely represent a fraction of the deployed

snares considering that a previous study in eastern Cambodia found that only 11-30% of snares are detected by ranger patrols (O'Kelly *et al.*, 2018). Therefore, it appears that local religious beliefs might indirectly affect Leopard populations in Southeast Asia, with taboos against consuming members of the Suidae family and species of similar appearance (e.g., Tapir *Tapirus indicus*) likely influencing poaching patterns, methods, and human pressures.

In addition to religious beliefs, geographical location may help explain the lower number of snares (Belecky and Gray, 2020) and higher number of Leopard detected in Malaysia and Indonesia. Countries in close proximity to Vietnam and China are more likely to experience the pressures of the demand for wildlife products, including those used in traditional medicine, as these two countries have contributed to an increase in demand for wildlife products and, generally, in commercial wildlife trade (Van Song, 2008). In eastern continental Southeast Asia (Vietnam, Cambodia, Laos) widespread and indiscriminate snaring often occurs at a high density (estimated density 110.7/km^2; Belecky and Gray, 2020). In these countries, local villagers often supplement their income by providing bushmeat to regional wildlife markets, which act as some of the primary drivers of poaching and exacerbate the situation. In countries such as Malaysia, where the socio-economic status is higher, distance to China and Vietnam is greater, and the law-enforcement presumably stronger, the benefits of engaging in illegal activities likely do not outweigh the consequences, which possibly results in locals engaging less often in criminal activities. However, further research is required to investigate in more detail the effects of social-economic status and cultural beliefs on Leopard populations in Southeast Asia.

3.5.1 Study limitations

We acknowledge that data from additional sites are required to obtain a more holistic picture of Leopard in the region, particularly considering that anthropogenic pressures, which seem to derive from complex, site-specific processes, appear to affect the species differently across sites. Because we essentially targeted priority sites of the subspecies, future standardized surveys may reveal an even bleaker picture of the Leopard in the region than we found. The precision of our parameter estimates could have been increased with additional sampling stations, particularly in areas where

despite our efforts the number of cameras deployed was limited due to logistical constraints or theft. To counter data sparsity, models that integrated the sparse data from the different study areas were used for the purpose of obtaining the best possible estimates. Although possible bias may have been introduced by sharing parameters, our density estimates provide baseline information relevant to assess population status of Leopard in Southeast Asia, where prior to this study, reliable SCR density estimates were only available for 3 areas. Similarly, we shared covariate coefficients in the habitat use (occupancy) model across several sites due to the sparse detection data. Consequently, only predictor variables (e.g., landcover) available for all study areas were used to explore Leopard habitat use; however, finer resolution layers may provide additional area-specific information not explored in this study. While we were able to estimate some region-specific (north and south) responses, potential unmodeled area-specific responses may have led to overall weak estimated relationships with covariates. In addition, the model approach used to investigate Leopard habitat use was fundamentally explorative, which may be considered poor strategy (Burnham and Anderson, 2002). However, due to the insufficient knowledge of the species in Southeast Asia, characterised by complex anthropogenic pressures that operate at multiple scales, such an explorative scheme seemed the most appropriate to ensure that relevant region-specific factors that influence Leopard habitat use were considered.

The camera-trap survey design (e.g., placement, sensitivity settings) likely reduced the detection probability of several small (<1 kg) species or those with arboreal or semi-arboreal habits, some of which were considered potential prey species of the Leopard, which could have influenced the index of overall prey availability. Moreover, area-specific differences (e.g., habitat structure) likely resulted in variation in detection probability of some of the species considered as potential prey. Although the levels of heterogeneity in detection probability and its implications for estimates of Leopard habitat use were somewhat diminished when grouping potential prey, future studies should investigate in more detail species-specific influences of prey on Leopard habitat use. Finally, because several study areas became inaccessible during the wet season, the research was exclusively conducted during the respective dry seasons; consequently, results only represent the latter season. Nevertheless, for a long-lived territorial species such as Leopard, dry season estimates should be

representative of density more generally, as major changes in density between seasons were not expected. Similarly, dry season estimates of habitat use should provide an adequate representation of the overall ecology of the species and its relationships with both humans and prey.

3.5.2 Conservation implications

Our findings suggest that the overall prognosis of the Leopard in the wider region is becoming increasingly bleak. Notably, our results indicate that several protected areas in Southeast Asia, most of which are chronically under-funded and under-protected, are suffering from high levels of anthropogenic pressures, which in turn have resulted in low Leopard densities even within the core zones of the protected areas. Because we essentially targeted priority sites of the subspecies, future standardized surveys may reveal an even grimmer picture of the Leopard in the region. Despite Leopard being legally protected in China and all Southeast Asian countries, current enforcement systems clearly lack capacity to tackle the threats to the species, particularly the poaching. In the absence of scaled-up enforcement and major societal changes that curb the demand for wildlife products, poaching likely will continue to expand as areas become increasingly defaunated, ultimately affecting more remote areas, which currently are less exposed to anthropogenic pressures (e.g., TNNP).

A broad array of actions is required to stem the current decline of Leopard and other wildlife throughout Southeast Asia. Importantly, the wildlife trade must be treated as a serious crime, and systematic, intensified, and more efficient law enforcement regimes must be developed. In addition, effective deterrents, such as adequate prosecution and conviction rates, need to be appropriately and consistently applied. Crucially, enforcement units must target both snare removal and prevention, with clear legal prohibition of snare use and possession. The success in tackling illegal human activities will necessitate commitment and support from governments, which through the strengthening of legislation, transboundary collaborations, and adherence to penalties proscribed by law, can act as deterrents, with the assistance from non-governmental organisations and civil society.

Although the Leopard is considered a highly adaptable species with the ability to persist in human dominated areas, results from our study areas showed that humans may have more insidious

effects on Leopard and the role it plays in ecosystems. Importantly, our findings suggest regional differences pertaining to poaching likely associated with cultural beliefs, geographical location, and socio-economic status between the Sundaic (i.e., Malaysia and Java) and eastern continental (i.e., Cambodia, Thailand) study areas, highlighting the importance of developing regional strategies that address area-specific anthropogenic pressures, including snaring intensity and target species. We recommend that core zones of protected areas are managed to ensure they truly represent areas optimally free of human disturbances in order to safeguard remaining animal populations, for which strong protected area management and enforcing zonation laws is critical. To maximise the effectiveness of interventions and make optimal use of limited conservation resources, it is essential that the species' remaining strongholds in the region are adequately protected. In addition, protected areas, which are a cornerstone in conservation, should be connected when possible with areas of sustainable use of resources. Eco-certified logging concessions potentially can provide connectivity, biodiversity protection and long-term maintenance of the ecological value of a forest, while offering financial benefits, such as selling timber at higher market prices to compensate for the reduced yields, that offset the profits offered by alternative forest uses such as plantations (Rayan and Linkie, 2015, Sollmann *et al.*, 2017). To ensure the survival of a viable Leopard metapopulation in the long term, the connectivity of subpopulations must be secured through establishing or maintaining corridors, as well as the conservation and recovery of the main prey species. Critically, education campaigns, human behavioural change interventions, and community outreach also are necessary to reduce demand and supply of bushmeat and wildlife parts at the provincial, national, and regional levels. Finally, Leopard population trends need to be monitored closely, given that a slight increase in poaching can greatly increase the probability of extinction of the species (Kenney *et al.*, 1995). Such monitoring also can be informative about the success or failure of specific conservation actions. Thus, we recommend the development of conservation measures and long-term monitoring programmes for this species in the region. Only with the implementation of timely and effective strategies will the long-term conservation of Leopard be feasible in Southeast Asia.

3.6 Acknowledgments

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Table 3.1 Summary information of Leopard (*Panthera pardus*) camera-trap surveys conducted in 7 sites across 4 countries throughout Southeast Asia: Srepok Wildlife Sanctuary (SrWS), Phnom Prich Wildlife Sanctuary (PPWS), Salakpra Wildlife Sanctuary (SaWS), Khlong Saeng Wildlife Sanctuary (KSWS), Taman Negara National Park (TNNP), Pasir Raja Selatan Forest Reserve (PR), Meru Betiri National Park (MBNP). CT = camera traps. North and South represent study site location in relation to the Isthmus of Kra.

	Country Study Area	**Survey period**	**No. of CT nights**	**Functional CT Locations**	**CT stolen (%)**	**Leopard Locations (%)**	**Melanistic individuals (%)**
North							
	Cambodia						
	SrWS	Dec 2015 - Feb 2016	2,973	46	6.1	28.3	0.0
	PPWS	Mar 2016 - May 2016	1,850	37	11.9	27.0	0.0
	Thailand						
	SaWS	Feb 2017 - Jun 2017	8,004	84	3.5	20.2	33.3
South							
	Thailand						
	KSWS	Mar 2017 - Jun 2017	3,597	44	4.3	0.0	-
	Malaysia						
	TNNP	Jun 2016 - Sep 2016	4,100	47	0.0	38.3	100.0
	PR	Aug 2016 - Nov 2016	2,405	30	0.0	16.7	100.0
	Indonesia						
	MBNP	Aug 2017 - Nov 2017	1,755	26	23.5	30.8	37.5
TOTAL			**24,684**	**314**	**6.3**	**26.3**	**50.0**

Table 3.2 Percentage of daylight records (DR), mean detection frequencies (MDF), estimates of coefficients of overlapping ($\widehat{\Delta}_1$) of Leopard (*Panthera pardus*) with main prey species and anthropogenic factors (i.e., illegal human activities, domestic animals; excluding tourist, rangers, researchers, and park staff) with 95% confidence intervals (CI) obtained from camera-trap surveys in Southeast Asia. Only study areas where Leopard was detected were included in the summary table: Srepok Wildlife Sanctuary (SrWS) and Phnom Prich Wildlife Sanctuary (PPWS), Cambodia; Salakpra Wildlife Sanctuary (SaWS), Thailand; Taman Negara National Park (TNNP) and Pasir Raja Selatan Forest Reserve (PR), Malaysia; Meru Betiri National Park (MBNP), Indonesia.

Isthmus of Kra	**Study Area**	**Leopard DR (%)**	**MDF**			**Coefficient of overlapping**								
						Anthropogenic			Cervids			Wild Pig		
			Anthropogenic	Leopard	Prey[1]	DR (%)	$\widehat{\Delta}_1$	CI	DR (%)	$\widehat{\Delta}_1$	CI	DR (%)	$\widehat{\Delta}_1$	CI
North	SrWS	12.5	2.790	0.007	0.178	81.7	0.34**	0.21 - 0.44	53.1	0.61	0.45 - 0.72	7.9	0.75*	0.63 - 0.90
	PPWS	38.7	0.615	0.011	0.428	85.7	0.53	0.39 - 0.65	55.4	0.77*	0.66 - 0.89	13.1	0.69	0.55 - 0.82
	SaWS	54.5	0.082	0.004	0.146	86.3	0.61	0.45 - 0.72	50.4	0.82*	0.79 - 0.98	48.1	0.81*	0.74 - 0.96
South	TNNP	81.0	0.002	0.010	0.172	83.3	0.54	0.32 - 0.85	88.1	0.77*	0.68 - 0.85	88.9	0.79*	0.71 - 0.90
	PR	90.0	0.000	0.003	0.120	NA	NA	NA	93.8	0.66	0.52 - 0.89	91.2	0.70*	0.60 - 0.99
	MBNP	85.7	0.132	0.010	0.434	81.3	0.77*	0.70 - 0.91	67.1	0.73*	0.61 - 0.86	80.0	0.74*	0.59 - 0.86

[1] All presumed preferred prey species based on previous dietary studies and weight range

** low overlap ($\widehat{\Delta}_1 \leq 0.35$)

* high overlap ($\widehat{\Delta}_1 \geq 0.70$)

Table 3.3 Posterior summaries (mean, standard deviation [SD] and 2.5th and 97.5th percentile) of density estimates (in individuals per 100 km^2) obtained using spatially explicit capture-recapture models fitted to camera-trapping data on Leopard (*Panthera pardus*) from 6 study areas across 4 countries in Southeast Asia: Srepok Wildlife Sanctuary (SrWS) and Phnom Prich Wildlife Sanctuary (PPWS), Cambodia; Salakpra Wildlife Sanctuary (SaWS), Thailand; Taman Negara National Park (TNNP) and Pasir Raja Selatan Forest Reserve (PR), Malaysia; Meru Betiri National Park (MBNP), Indonesia.

	Null model				**Full model**			
Study area	Mean	SD	2.50%	97.50%	Mean	SD	2.50%	97.50%
SrWS	0.56	0.20	0.26	1.02	0.48	0.20	0.17	0.87
PPWS	0.88	0.34	0.39	1.68	0.92	0.83	0.32	2.32
SaWS	0.23	0.11	0.09	0.48	0.21	0.11	0.09	0.43
TNNP	2.63	0.86	1.25	4.60	4.82	1.77	1.71	8.22
PR	0.97	0.54	0.30	2.35	1.23	0.79	0.23	2.73
MBNP	4.74	1.72	2.12	8.77	4.60	2.33	1.41	10.32

Table 3.4 Posterior means, standard deviation (SD) and 75% Bayesian credible intervals (BCI) for coefficients (β) describing the effect of covariates on the probability of habitat use and detection of Leopard (*Panthera pardus*) in Southeast Asia; estimated with occupancy models fitted to camera-trapping data on Leopard from 6 study areas across 4 countries in Southeast Asia. Information about the covariates can be found in Appendix 3.1.

Model component	Covariate	Mean	SD	75% BCI	
Detection					
	(Intercept)	-0.903	0.466	-1.413	-0.432
	Effort	0.479	0.180	0.268	0.681
	Road	-0.520	0.575	-1.134	0.170
Habitat Use					
	(Intercept)	-0.735	0.464	-1.190	-0.341
	Distance to Water (m)	-0.216	0.303	-0.537	0.139
	Elevation (m)	-0.585	0.293	-0.923	-0.264
	Forest Loss	0.308	0.262	-0.019	0.564
	Illegal Human activity*	-0.127	0.400	-0.515	0.202
	NDVI**	0.536	0.387	0.054	0.878
	Preferred prey*	-0.264	0.243	-0.504	0.013

* Detection frequencies (aggregated independent capture events per total trap days)
** Normalized Difference Vegetation Index

Table 3.5 Estimates of Moran's I statistic (MI) and associated *p*-values (*p*) at different neighbourhood distances (i.e., M1-M7) for residuals from habitat use model of Leopard (*Panthera pardus*) recorded with camera traps in 6 different study areas in Southeast Asia (i.e., A1-A6). Significant Moran's I ($p \leq 0.05$) is shown in bold font.

Distances	**Study Areas**											
	A1		A2		A3		A4		A5		A6	
	MI	*p*	MI	*p*	MI	*p*	MI	*p*	MI	*p*	MI	*p*
M1	-0.088	0.706	0.004	0.450	0.070	0.303	0.222	**0.023**	-0.030	0.555	0.004	0.418
M2	0.055	0.191	-0.026	0.466	-0.006	0.372	-0.109	0.862	-0.161	0.895	-0.009	0.441
M3	-0.041	0.576	-0.125	0.979	-0.001	0.265	-0.106	0.967	-0.008	0.315	0.015	0.175
M4	-0.038	0.619	-0.060	0.781	0.014	0.130	-0.079	0.965	-0.028	0.378	-0.014	0.477
M5	-0.056	0.859	-0.042	0.706	-0.037	0.431	0.012	0.098	-0.041	0.542	-0.026	0.784
M6	-0.026	0.512	-0.029	0.463	-0.043	0.573	-0.033	0.708	-0.038	0.546	-0.018	0.650
M7	-0.020	0.407	-0.028	0.474	-0.054	0.859	-0.015	0.248	-0.036	0.515	-0.012	0.435

Table 3.6 Leopard (*Panthera pardus*) density estimates obtained using spatially explicit capture-recapture models. We used the first five pages of Google Scholar of studies published between 2012 and 2020 in our assessment. Under each continent, densities are listed from lowest to highest estimates.

Continent	Country	Density estimate (Leopard/100 km^2)	SD (SE)	Subspecies	Reference
Asia	Thailand	0.23	0.11	*P. pardus delacouri*	This study
Asia	Cambodia	0.56	0.20	*P. pardus delacouri*	This study
Asia	China	0.62	0.15	*P. pardus orientalis*	Qi *et al.* (2015)
Asia	India	0.74	0.18	*P. pardus fusca*	Noor *et al.* (2020)
Asia	Cambodia	0.88	0.34	*P. pardus delacouri*	This study
Asia	Malaysia	0.97	0.54	*P. pardus delacouri*	This study
Asia	Cambodia	1.00	0.40	*P. pardus delacouri*	Rostro-García *et al.* (2018)
Asia	Nepal	1.50	0.49	*P. pardus fusca*	Kandel *et al.* (2020)
Asia	Russia	1.62	-	*P. pardus orientalis*	Lukarevskiy and Lukarevskiy (2019)
Asia	China	2.00	0.53	*P. pardus japonensis*	Yang *et al.* (2020)
Asia	Thailand	2.60	1.20	*P. pardus delacouri*	Ngoprasert *et al.* (2017)
Asia	Malaysia	2.63	0.86	*P. pardus delacouri*	This study
Asia	India	2.82	1.20	*P. pardus fusca*	Selvan *et al.* (2014)
Asia	Malaysia	3.06	0.91	*P. pardus delacouri*	Hedges *et al.* (2015)
Asia	India	3.40	0.82	*P. pardus fusca*	Borah *et al.* (2014)
Asia	Nepal	3.48	0.83	*P. pardus fusca*	Thapa *et al.* (2014)
Asia	Cambodia	3.60	1.00	*P. pardus delacouri*	Gray and Prum (2012)
Asia	Indonesia	4.74	1.72	*P. pardus melas*	This study
Asia	India	4.84	1.22	*P. pardus fusca*	Athreya *et al.* (2013)
Asia	India	8.40	1.40	*P. pardus fusca*	Mondal *et al.* (2012b)
Asia	India	9.76	3.50	*P. pardus fusca*	Harihar *et al.* (2011)
Asia	Bhutan	10.00	-	*P. pardus fusca*	Goldberg *et al.* (2015)
Asia	Indonesia	12.80	1.99	*P. pardus melas*	Rahman *et al.* (2018)
Asia	India	13.01	2.31	*P. pardus fusca*	Kalle *et al.* (2011)
Asia	Sri-Lanka	14.70	6.30	*P. pardus kotiya*	Kittle *et al.* (2017)
Africa	South Africa	1.18	0.29	*P. pardus pardus*	Devens *et al.* (2019)
Africa	South Africa	1.61	0.62	*P. pardus pardus*	Ramesh *et al.* (2017)
Africa	Mozambique	2.60	0.96	*P. pardus pardus*	Strampelli *et al.* (2020)
Africa	South Africa	3.55	1.04	*P. pardus pardus*	Braczkowski *et al.* (2016)
Africa	Tanzania	4.22	-	*P. pardus pardus*	Havmøller *et al.* (2019)
Africa	South Africa	4.56	1.35	*P. pardus pardus*	Swanepoel *et al.* (2015)
Africa	Zimbabwe	5.28	0.89	*P. pardus pardus*	du Preez *et al.* (2014)
Africa	South Africa	5.34	0.02	*P. pardus pardus*	Williams *et al.* (2017)
Africa	South Africa	5.35	2.93	*P. pardus pardus*	Swanepoel *et al.* (2015)
Africa	Tanzania	5.41	0.00	*P. pardus pardus*	Allen *et al.* (2020)
Africa	South Africa	6.59	5.20	*P. pardus pardus*	Swanepoel *et al.* (2015)
Africa	South Africa	8.40	1.03	*P. pardus pardus*	Ramesh *et al.* (2017)
Africa	South Africa	10.73	3.32	*P. pardus pardus*	Chase Grey *et al.* (2013)
Africa	South Africa	11.80	2.60	*P. pardus pardus*	Balme *et al.* (2019)
Africa	Kenya	12.03	3.30	*P. pardus pardus*	O'Brien and Kinnaird (2011)
Africa	Namibia	14.51	-	*P. pardus pardus*	Noack *et al.* (2019)

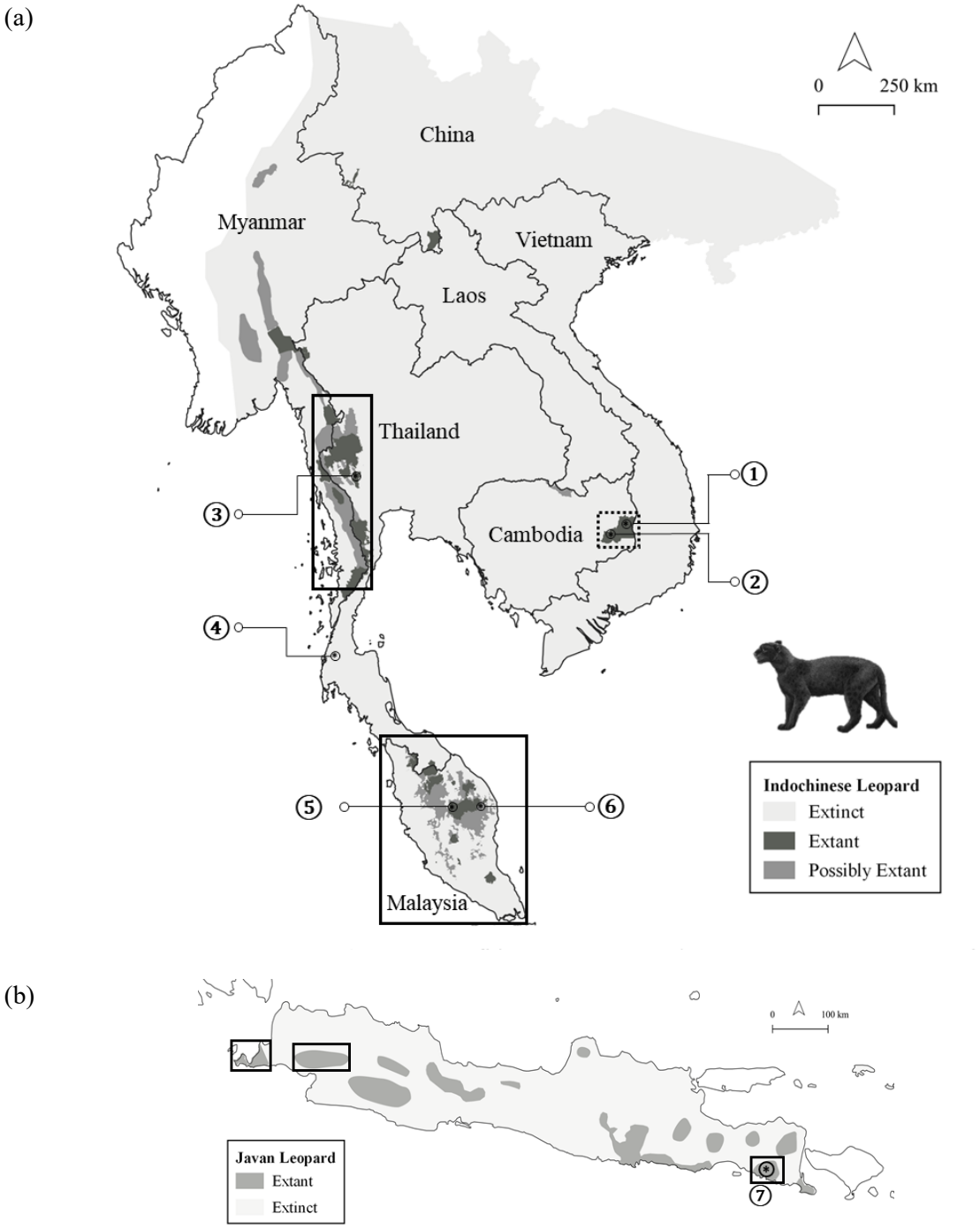


Figure 3.1 The current (confirmed and potential) estimated distribution of the: a) Indochinese (*Panthera pardus delacouri*) and b) Javan (*P. pardus melas*) Leopard in Southeast Asia. Strongholds are indicated with solid rectangles, an additional priority site in eastern Cambodia is indicated with a dashed rectangle. Location of the study areas where surveys were conducted are shown with a number: (1) Srepok Wildlife Sanctuary, (2) Phnom Prich Wildlife Sanctuary, (3) Salakpra Wildlife

Sanctuary, (4) Khlong Saeng Wildlife Sanctuary, (5) Taman Negara National Park, (6) Pasir Raja Selatan Forest Reserve, (7) Meru Betiri National Park.



Figure 3.2 Melanistic Indochinese Leopard (*Panthera pardus delacouri*) photographed in Taman Negara National Park, Malaysia, during this study using a Panthera V6 camera trap with infrared flash.

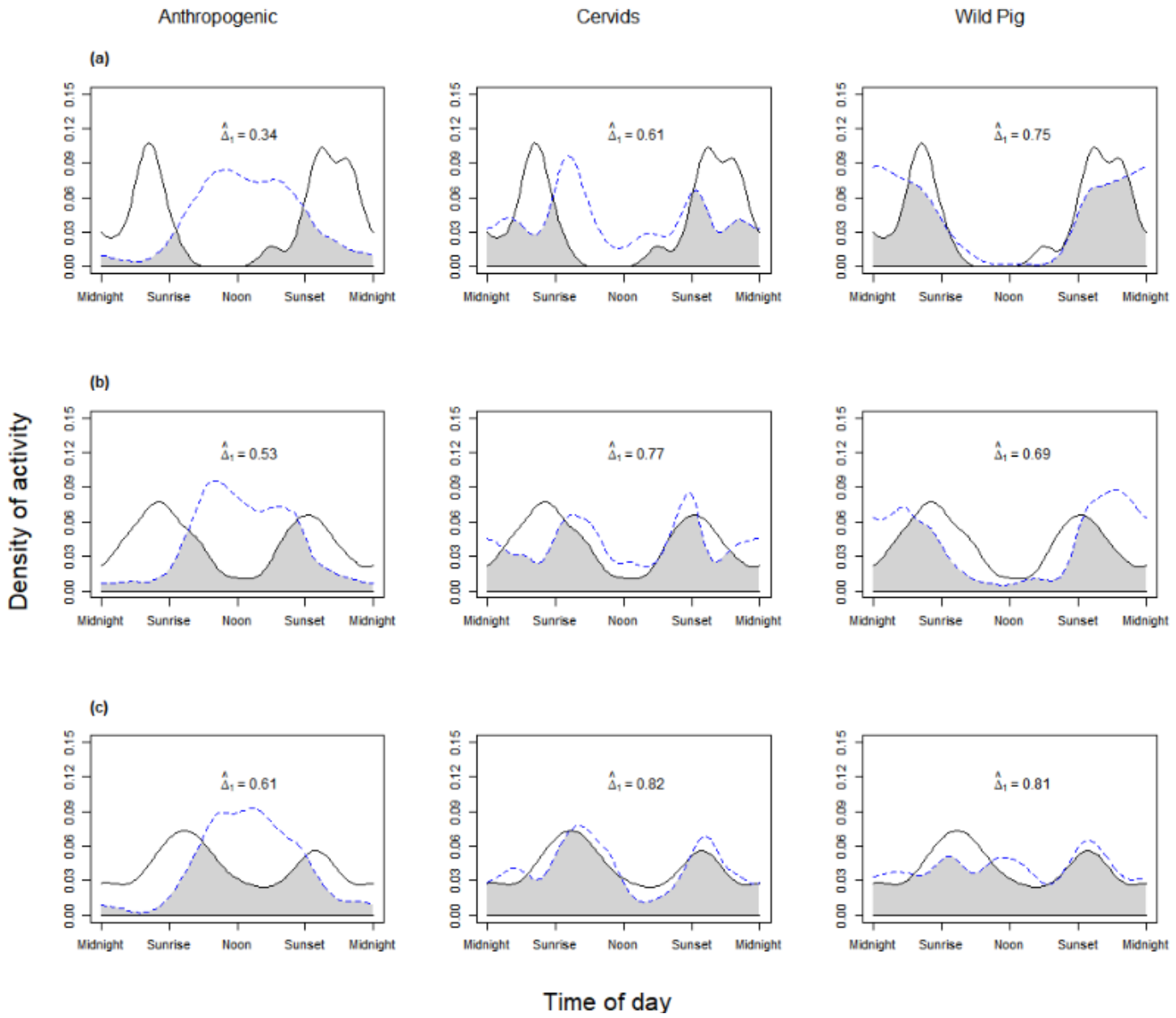

Anthropogenic
Cervids
Wild Pig
(a)
(b)
(c)
Density of activity
Time of day
Midnight
Sunrise
Noon
Sunset
0.00
0.03
0.06
0.09
0.12
0.15
$\hat{\Delta}_1$ = 0.34
$\hat{\Delta}_1$ = 0.61
$\hat{\Delta}_1$ = 0.75
$\hat{\Delta}_1$ = 0.53
$\hat{\Delta}_1$ = 0.77
$\hat{\Delta}_1$ = 0.69
$\hat{\Delta}_1$ = 0.61
$\hat{\Delta}_1$ = 0.82
$\hat{\Delta}_1$ = 0.81

Figure 3.3 Kernel density estimates of diel activity patterns of Leopard (*Panthera pardus*) and anthropogenic factors, cervids or Wild Pig (*Sus scrofa*) in the northern sites: a) Srepok Wildlife Sanctuary, Cambodia; b) Phnom Prich Wildlife Sanctuary, Cambodia; c) Salakpra Wildlife Sanctuary, Thailand. Solid black lines are kernel-density estimates of Leopard, whereas dashed blue lines represent kernel-density estimates of anthropogenic factors, cervids or Wild Pig. The coefficients of overlapping ($\widehat{\Delta}_1$) are represented by the shaded areas.

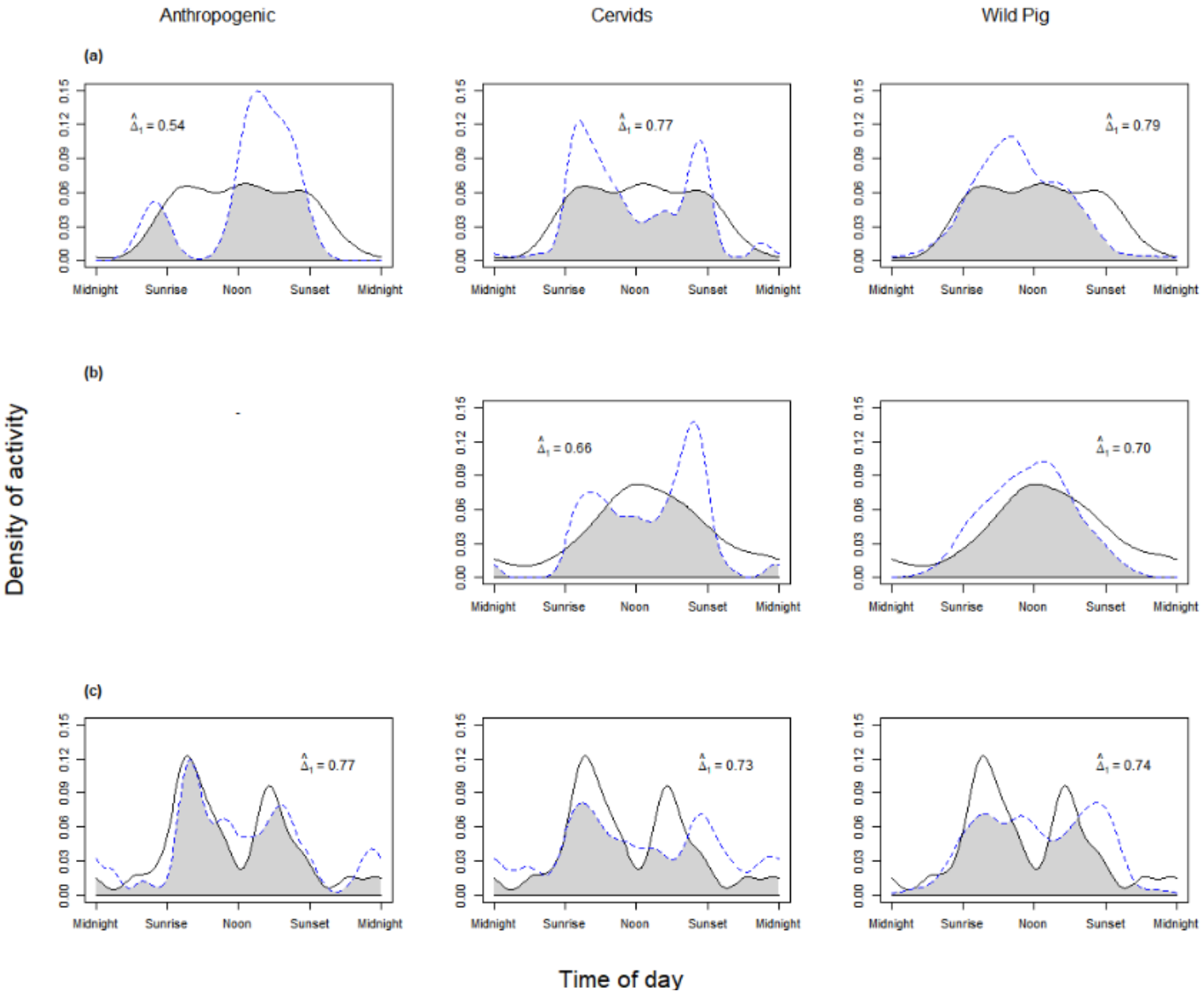

Anthropogenic
Cervids
Wild Pig
(a)
(b)
(c)
Density of activity
Time of day
Midnight
Sunrise
Noon
Sunset
0.00
0.03
0.06
0.09
0.12
0.15
$\hat{\Delta}_1$ = 0.54
$\hat{\Delta}_1$ = 0.77
$\hat{\Delta}_1$ = 0.79
$\hat{\Delta}_1$ = 0.66
$\hat{\Delta}_1$ = 0.70
$\hat{\Delta}_1$ = 0.77
$\hat{\Delta}_1$ = 0.73
$\hat{\Delta}_1$ = 0.74

Figure 3.4 Kernel density estimates of diel activity patterns of Leopard (*Panthera pardus*) and anthropogenic factors, cervids or Wild Pig (*Sus scrofa*) in the southern sites: a) Taman Negara National Park, Malaysia; b) Pasir Raja Selatan Forest Reserve, Malaysia; c) Meru Betiri National Park, Indonesia. Solid black lines are kernel-density estimates of Leopard, whereas dashed blue lines represent anthropogenic factors, cervids or Wild Pig. The coefficient of overlapping ($\widehat{\Delta}_1$) is represented by the shaded area.

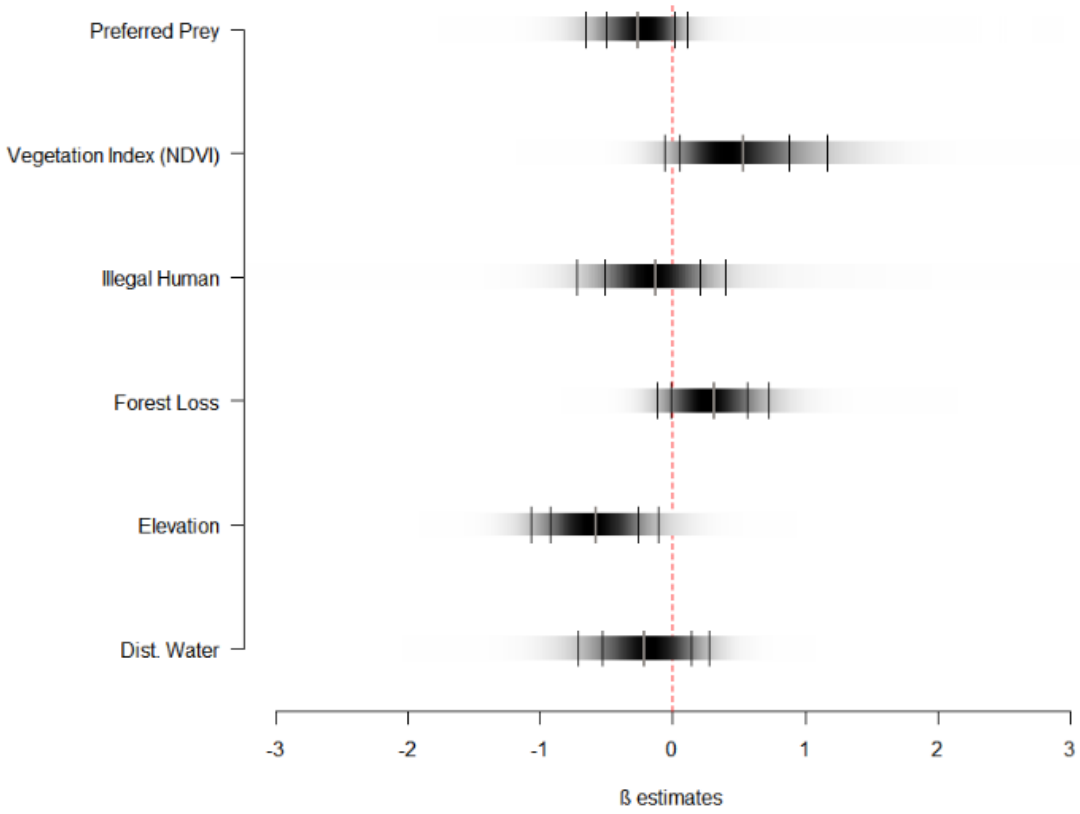


Figure 3.5 Bayesian posterior samples plot for coefficients (β) of covariates affecting the probability of habitat use by Leopard (*Panthera pardus*) in Southeast Asia, based on results from an occupancy model fitted to camera-trapping data on Leopard from 6 study areas across 4 countries in Southeast Asia. The strips are shaded in proportion to the posterior probability density, with darkest shade indicating the maximum density. Grey vertical lines denote the posterior means, and black vertical lines the 75% and 90% highest (posterior) density intervals. Zero (red dotted line) partitions the direction of the covariate effect.

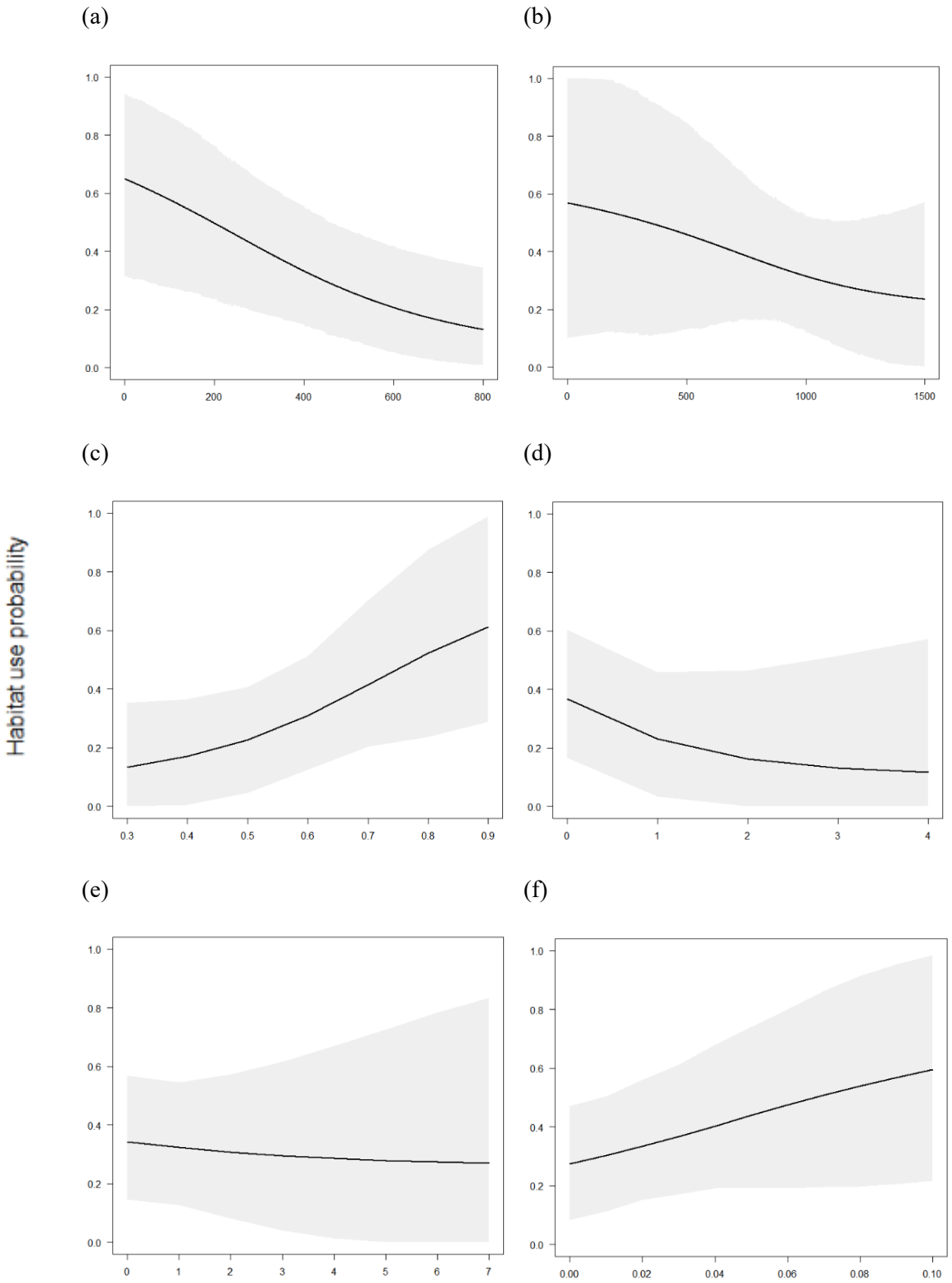


Figure 3.6 Probability of Leopard (*Panthera pardus*) habitat use as a function of environmental and anthropogenic predictors, based on results from an occupancy model fitted to camera-trapping data on Leopard from 6 study areas across 4 countries in Southeast Asia. The solid black lines depict the posterior mean, and the light grey polygons depict the 95% Bayesian credible intervals. The

predictors used were: (a) elevation (m); (b) distance to river (m); (c) Normalized Difference Vegetation Index (NDVI); (d) detection frequency of presumed preferred prey; (e) detection frequency of anthropogenic factors (i.e., illegal human activities and domestic animals); (f) forest loss. Information about the covariates can be found in Appendix 3.1.

3.7 Supplementary Materials

Appendix 3.1

Based on *a priori* knowledge and previous studies on Leopard (*Panthera pardus*) and similar large carnivores (Gavashelishvili and Lukarevskiy, 2008, Rahman *et al.*, 2018, Ratnayeke *et al.*, 2018, Rayan and Linkie, 2015, Wang *et al.*, 2018), we selected a set of environmental and anthropogenic covariates in order to assess Leopard habitat use. Top-performing scales and covariates were selected using maximum likelihood inference. All models were compared using Akaike's Information Criterion (AIC; Burnham and Anderson, 2004) and fitted using single-season, single-species occupancy models with the R package 'unmarked' v 1.0.1 (Fiske and Chandler, 2011). Specifically, a 3-step approach was adopted to reduce the number of combinations of every possible covariate. First, the detection probability p was modelled by running all possible combinations of detection covariates (i.e., effort, study area, on/off road location of camera traps) while keeping site occupancy ψ constant but with study area as a fixed effect on ψ to preserve potential structure in the occupancy component. Second, we retained relevant detection covariates and model habitat use probability in relation to the site covariates (Long *et al.*, 2011), for which we performed multi-scale optimisation. To identify the most relevant scale to each covariate (Table A3.1), we fitted univariate models, with the different radii distances considered (i.e., 0.3, 1, 2, 4, 8, 15, and 30 km) selected to represent ecological responses of Leopard across scales relevant to meet the daily requirements of the species, from resources within habitat patches, to reported distances travelled daily during dry season (29 km^2; Hubel *et al.*, 2018), and considering the movement parameter obtained in this study. We identified the top-performing scale for each site covariate, and tested for multicollinearity across the covariates at their best scales by calculating Pearson's correlation index, considering pair-wise combinations with a correlation coefficient $r > 0.7$ as strongly correlated (Dormann *et al.*, 2013). We then fitted multivariate models considering all possible combinations of the site covariates at their best scales, as well as the detection frequencies of anthropogenic factors and presumed preferred prey (see below for more details). We also performed a goodness-of-fit test for the top-performing

multivariate model with 1,000 bootstraps (MacKenzie and Bailey, 2004). Prior to modelling, all covariates were standardized to a zero mean and unit standard deviation.

We classified all photographs of Binturong (*Arctictis binturong*), Eld's Deer (*Rucervus eldii*), Hog Badger (*Arctonyx collaris*), Hog Deer (*Axis porcinus*), Muntjac (*Muntiacus* spp.), primates, Sambar (*Rusa unicolor*), Serow (*Capricornis sumatraensis*) and Wild Pig (*Sus scrofa*), as presumed preferred prey, considering previous dietary studies of Leopard conducted in the region (Grassman, 1999, Rabinowitz, 1989, Rostro-García *et al.*, 2018, Steinmetz *et al.*, 2013) and on previous results showing that Leopard preferentially prey on species within a weight range of 10-40 kg (Hayward *et al.*, 2006). Anthropogenic factors included records of illegal activities (e.g., logging, poaching, motorbikes), as well as records of domestic animals (i.e., dogs and cattle), which typically were accompanied by illegal intruders in our study areas. We excluded photographs of researchers and park staff, which, although they may have temporally caused disturbances, were not associated with major anthropogenic stressors. In addition, both sites in Malaysia had tourists who were accompanied by guides and restricted to certain tails. We excluded tourists from the anthropogenic factors because previous research showed that tourists did not affect diel activity patterns of mammals, including the Leopard, in Malaysian parks (Ota *et al.*, 2019), where there is typically less illegal human activity compared to the northern sites. Detection frequencies were calculated by aggregating notionally independent photographs and dividing by the number of days the camera-trap station was functional multiplied by 100. We considered independent events as photographs of the same species (or illegal human activity) taken >60 minutes apart at the same station to avoid inflated counts caused by repeated detections of the same event.

Table A3.1 Environmental and anthropogenic site covariates screened to model habitat use (occupancy) by Leopard (*Panthera pardus*) in Southeast Asia. Each covariate has information about the expected influence on the probability of habitat use by Leopard in Southeast Asia (Hypothesized relationship to ψ), metric calculated, native resolution and data source. FM = focal mean obtained through circular window, DF = detection frequency (aggregated independent capture events per total trap days multiplied by 100), ED = Euclidian distance.

Category Covariate	**Hypothesized relationship to ψ**	**Metric**	**Native Resolution**	**Source**
Land cover				
Agricultural	-	FM	300m	ESA CCI Land Cover layer - ESA (2020)
Urban Areas	-	FM	300m	ESA CCI Land Cover layer - ESA (2020)
Forested Areas	+	FM	300m	ESA CCI Land Cover layer - ESA (2020)
Other Vegetation	+	FM	300m	ESA CCI Land Cover layer - ESA (2020)
Site productivity				
Enhanced Vegetation Index (EVI)	+	FM	250m	MOD13Q1 - Didan (2015)
Normalized Difference Vegetation Index (NDVI)	+	FM	250m	MOD13Q1 - Didan (2015)
Mean monthly Gross Primary Productivity (GPP)	+	FM	500m	MOD17A2 - Running *et al.* (2015)
Monthly Precipitation	+	FM	0.25 degrees	PERIANN-CDR - Sorooshian *et al.* (2014)
% Forest Cover	+	FM	30m	Hansen *et al.* (2013)
Human disturbance				
Human Presence	-	DF	NA	Camera-trap data from this study
Forest Loss	-	FM	30m	Hansen *et al.* (2013)
Distance to Settlements	+	ED	NA	OpenStreetMap contributors[a] and manually digitized
Distance to Roads	+	ED	NA	OpenStreetMap contributors[a] and manually digitized
Topography				
Elevation	-	FM	30m	Shuttle Radar Topography Mission (SRTM) DEM[b]
Slope	-	FM	30m	Shuttle Radar Topography Mission (SRTM) DEM[b]

Terrain Ruggedness Index	-	FM	30m	Shuttle Radar Topography Mission (SRTM) DEM[b]
Others				
Distance to Rivers	-	ED	NA	HydroRIVERS v1.0 - Lehner and Grill (2013)
Distance to Protected Area Boundary	+	ED	NA	UNEP-WCMC and IUCN (2020) and local NGOs
Preferred Prey Presence	+	DF	NA	Camera-trap data from this study

[a] https://www.openstreetmap.org/copyright
[b] https://lta.cr.usgs.gov

CHAPTER 4

Camera trapping in low-density populations: can we get reliable density estimates?

4.1 Abstract

Population parameters, fundamental to understanding, managing, and conserving animal populations, can be directly estimated using spatially explicit capture-recapture (SCR) models. Developments in SCR methods have put camera traps, commonly used to non-invasively study animal populations, at the forefront of conservation programs, particularly of rare, elusive, and wide-ranging species. Despite the importance of appropriate sampling designs and the widespread adoption of SCR methods, little guidance exists on how to practically implement such studies to generate reliable estimates, and their performance in low-density populations remains little understood. Here we used simulated and empirical data under a range of ecologically realistic scenarios and commonly used study designs to investigate the performance of SCR models in low-density populations surveyed using camera traps. Specifically, we evaluated the effects of different number of camera-trap stations, configuration (uniform and multi-cluster layout), presence or absence of spatial noise (jittering), spacing between stations (2 km and 4 km), and presence or absence of a density edge effect in very low-density (VLD) and moderately low-density (MLD) populations of Leopard (*Panthera pardus*), the most studied species using camera traps and a resilient carnivore often used as a surrogate for conservation actions. Our simulations showed that performance of SCR models varied based on the magnitude of Leopard density and sampling design, with larger number of camera traps and wider spacing between stations producing better estimates. Performance of SCR models was better under VLD scenarios than MLD scenarios, the latter of which often were biased high and imprecise under the conditions studied. Our results using empirical data suggested that in general precision decreased and bias increased with decreasing number of camera-trap stations, particularly when less than 20 stations were used. Based on our findings, it is likely that some camera-trap studies targeting low-density populations may not be meeting the requirements necessary to

produce unbiased population parameter estimates, likely resulting in overestimates of densities that consequently can be counterproductive for the conservation of the target species. We suggest integrating pilot studies with simulations or similar assessment approaches for *a priori* evaluation of study designs to facilitate the applicability of SCR methods when studying low-density populations using camera traps.

Keywords: Camera traps, density, edge effect, large carnivores, Leopard, low-density populations, *Panthera pardus*, sampling design, SCR, spatially explicit capture-recapture, Southeast Asia.

4.2 Introduction

Terrestrial mammals worldwide are experiencing an unprecedented collapse in population sizes and geographical ranges (Ripple *et al.*, 2016). Large carnivores are most at risk (Cardillo *et al.*, 2005, Wolf and Ripple, 2017), with 61% of the world's large carnivore species being threatened with extinction (Ripple *et al.*, 2014). Given the severity of threats, the preservation of large carnivores and the stabilizing effects they play in ecosystems demands immediate conservation action, which in turn urgently requires multifaceted information. Estimating population parameters, such as abundance and density, is fundamental to understanding and conserving populations, particularly for species of conservation concern (Sollmann *et al.*, 2012, Sun *et al.*, 2014, Wilton *et al.*, 2014). Knowledge about population parameters is essential to assess the status of a species, as well as to provide baseline information for future research, direct and evaluate conservation actions, and guide resource allocation.

Both population size and density can directly and most reliably be estimated using spatially explicit capture-recapture (hereafter SCR) models (Borchers and Efford, 2008, Efford, 2004, Royle *et al.*, 2014, Royle and Young, 2008), which have become the conventional method for analysing spatially indexed encounter history data collected from sampling devices or "traps" (e.g., camera traps, hair snares, acoustic recording devices). By explicitly modelling the spatial organisation of individuals relative to the sampling devices, as well as considering the location of individual detections, SCR models account for imperfect detection and variation in detection among individuals due to differential overlap with the sampling devices. These models yield spatially-explicit estimates of abundance which can readily be translated into population density, representing a more robust advance over traditional, non-spatial approaches (Chandler and Royle, 2013, Royle *et al.*, 2014). In general, to estimate population parameters with accuracy and precision, empirical and theoretical work suggests large numbers of encountered individuals and spatial recaptures (i.e., when the same individual is detected at multiple locations) are necessary (Paterson *et al.*, 2019, Sollmann *et al.*, 2012, Sun *et al.*, 2014). However, this can be a challenging endeavour when studying large carnivores which often persist at low densities, are cryptic and elusive in nature, and have large home ranges that are not uniformly distributed over vast

landscapes that may include inaccessible habitat. These ecological characteristics pose numerous challenges to estimating population parameters, often inducing heterogeneity in detection probabilities among individuals and across space, and resulting in overall low detection probabilities. This in turn generates data sets that are sparse in terms of the number of individuals and spatial recaptures, and that potentially contain insufficient information to reliably estimate population parameters. Accordingly, previous studies have suggested that insufficient information, arising from low detection probabilities, individual heterogeneity or the sampling strategy used, can result in strongly biased and imprecise population parameter estimates (Howe *et al.*, 2013, Keiter *et al.*, 2017, Paterson *et al.*, 2019, Tobler and Powell, 2013).

The accuracy of the estimates can be improved through the sampling design, which directly impacts the amount of information contained in the data and overall performance of the estimators (Dupont *et al.*, 2020). Two of the most critical elements of sampling design in spatial capture-recapture surveys are the spatial configuration (i.e., layout) and the spacing among the traps within a trap array (Royle *et al.*, 2014, Sun *et al.*, 2014). In general, sample size in SCR is comprised of the total number of individuals captured, as well as the number of recaptures and of spatial recaptures, which provide information about baseline encounter probability (p_0), and the spatial scale parameter (σ), respectively (Royle *et al.*, 2014). Because SCR models require a sufficient number of individuals captured at multiple locations, SCR survey designs frequently represent a compromise between obtaining a sufficient sample size of unique individuals and of spatial recaptures. These two objectives often contradict one another in practice with regards to their requirements for trap spacing (Royle *et al.*, 2014). With an often restricted number of traps due to logistical and/or monetary considerations, a sampling trade-off between spatial extent and trap spacing frequently occurs (Royle *et al.*, 2014, Sun *et al.*, 2014). Consequently, optimising this trade-off, particularly when resources are limited, is not trivial. Therefore, considerations regarding the configuration and spatial extent of the sampling array are critical when designing effective SCR studies. This is particularly true when studying low-density, wide-ranging large carnivores given the amount of effort and resources required for such surveys.

Despite the importance of appropriate sampling design and the widespread adoption of SCR models, little guidance exists on how to practically implement such studies to generate reliable population estimates. Simulations are a valuable tool for improving knowledge by allowing the comprehensive evaluation of multiple sampling design scenarios, thereby providing information to an extent usually not available from empirical data (Kristensen and Kovach, 2018, Royle *et al.*, 2014). Previous studies using American Black Bear *Ursus americanus* (Clark, 2019, Sollmann *et al.*, 2012, Sun *et al.*, 2014, Wilton *et al.*, 2014) and a few other species (Kristensen and Kovach, 2018, Paterson *et al.*, 2019, Tobler and Powell, 2013) as case studies have evaluated the effectiveness of SCR study design using simulations. Surprisingly, to date the effects of spatial sampling design on SCR models have not been tested in low-density populations, including in those of some the most charismatic and well-studied species (e.g., large felids). Nonetheless, it is likely that the importance of study design becomes particularly pressing under such marginal-information situations, where identifying the best compromise between different trap design requirements may be particularly significant.

Camera traps have become an important and commonly used tool to non-invasively study animal populations, particularly of large carnivores (Burton *et al.*, 2015, Green *et al.*, 2020, Karanth and Nichols, 1998, Rowcliffe and Carbone, 2008, Trolliet *et al.*, 2014). Compared to other monitoring tools, camera-trap surveys can be the most efficient way of monitoring these difficult to study species, which puts them at the forefront of population monitoring programs, especially of individually recognizable species (e.g., large felids; Green *et al.*, 2020, Meek *et al.*, 2014). In spite of camera traps being one of the most common sampling devices used to collect carnivore data, few studies have evaluated the performance of SCR models (i.e., influence on parameter estimation) and the specifics for optimal sampling design when studying low-density populations using this type of detector, thereby becoming virtually a heuristic process (Dupont *et al.*, 2020). In accordance, a review of the study design used in camera-trap surveys of Jaguar (*Panthera onca*), one of the most studied species using this methodology, alarmingly concluded that mostly due to inadequate sampling design, a majority of surveys did not meet the requirements necessary to produce unbiased estimates, likely resulting in overestimates of densities (Tobler and

Powell, 2013). Clearly, further investigation into SCR performance when studying low-density populations of large carnivores with camera traps is warranted to ensure reliable population parameter estimates.

The aim of this study is to use both simulated and empirical data to evaluate the performance of SCR models in estimating density when studying low-density populations of large carnivores surveyed with camera traps using commonly used study designs. For that we used data on a Critically Endangered subspecies of Leopard (*Panthera pardus*) endemic to Southeast Asia – the Indochinese Leopard (*P. pardus delacouri*; Rostro-García *et al.*, 2019). The Leopard, one of the most studied species using camera traps (Green *et al.*, 2020), is considered to be a relatively resilient large carnivore that is often used as a surrogate for conservation outcomes, and as a suitable model for investigating issues that affect the persistence of carnivore populations more widely (Balme *et al.*, 2010b, Sergio *et al.*, 2008). We were primarily interested in evaluating the performance of SCR designs under a range of ecologically realistic scenarios, especially extremely low densities. Although currently typical of certain regions such as Southeast Asia, these low-density scenarios are likely to become increasingly more prevalent throughout the world as anthropogenic pressures increase and wildlife populations decline. Protected area borders and peripheries often can act as population sinks or ecological traps where, in areas of otherwise suitable resources, a disproportionately high mortality from humans can occur (Balme *et al.*, 2010b, Woodroffe and Ginsberg, 1998), which often results in lower animal densities compared to the core zones (Balme *et al.*, 2010b, Havmøller *et al.*, 2019, Kittle *et al.*, 2021). This in turn can have detrimental effects on vital rates, and cause the decline and possibly extinction of animal populations within protected areas (Balme *et al.*, 2010b, Woodroffe and Ginsberg, 1998). Therefore, we were also interested in evaluating how the performance of commonly used study designs changed when studying low-density populations affected by an edge effect. To our knowledge, our study is the first evaluation of SCR performance on low-density populations surveyed using camera traps, and as such provides applicable information and insights relevant to other large carnivore studies.

4.3 Materials and methods

We were primarily interested in evaluating the performance of commonly used SCR designs under a range of ecologically realistic scenarios typical of low-density carnivore populations found throughout Southeast Asia. For this, we used both simulated and empirical data.

4.3.1 Simulation study

Spatially explicit capture-recapture methods combine two submodels that each contribute to the sampling variance of the estimates: a model for the spatial distribution of individuals (ecological model) and a model for the spatial detection process (observational model, Efford and Boulanger, 2019). In the ecological model, conceptualised as a spatial point process, the individuals are represented by unique and at least temporally persistent points (i.e., activity centres), with animal density being the intensity of the point process, which can in turn be homogenous or heterogenous (Efford and Boulanger, 2019, Royle *et al.*, 2014). In the observational component, SCR models assume a radial decline in the detection probability with increasing distance between a trap and an individual's activity centre, and allow to accommodate variation in detection probability with regards to individual, detectors, and time (Efford and Boulanger, 2019, Royle *et al.*, 2014). We were interested in how the performance of commonly used study designs varied as a function of: 1) density pattern (homogeneous and heterogeneous), and 2) magnitude of density (very low or moderately low). The design of the simulations, as well as the underlying parameters governing the data generating process, were based on prior empirical work on Leopard in the wider region (Chapter 3, Hedges *et al.*, 2015, Rostro-García *et al.*, 2018).

State-space & density patterns – We based our simulations on a fixed 1,024 km^2 (32 x 32) simulated study area, which represents a typical study area size in the region. The spatial extent of this fixed-square simulated study area was held constant to mimic field conditions. We assumed a 1-km^2 pixel size of non-overlapping cells, each of which could potentially represent the home range centre of an individual. Previous studies investigating the effect of sampling design on SCR performance typically assumed a

homogenous distribution of individuals over the landscape (but see Dupont *et al.*, 2020, Efford and Fewster, 2013). However, we were also interested in evaluating the performance of the designs in the presence of a non-uniform density pattern, as this likely represented a more realistic scenario in anthropogenically disturbed areas. Therefore, we considered two main spatial density patterns: a homogeneous scenario and a heterogeneous scenario with an edge effect. In both cases, individuals were randomly distributed in the area according to a binomial point process (Royle *et al.*, 2014). For the spatially-varying scenario, we generated an edge effect in our population by simulating a heterogenous point process where density depended on the distance to the edge of the study area. For this we defined a covariate *X* for edge distance, which provided the distance from the edge of the study area to the centre point of each pixel. We defined the probability of an activity centre (of a Leopard) being located in pixel *i* as:

$$Prob_i = \frac{e^{\beta_* X_i}}{\sum e^{\beta_* X_i}}$$

where X_i is the value of the distance covariate for pixel *i*, and β is the coefficient of the effect of edge distance on point intensity, such that a decline in density is generated towards the edge of the study area. We assumed that when existent, the effect of edge extended up to 5 km into the study area and with a value of β chosen such that it caused a total decline of about 40% in density from the core to the edge, based on a previous study that assessed the extent and impact of edge effects on the species (Balme *et al.*, 2010b). We achieved this by censoring the values of the covariate *X* for all pixels that were at a distance >5 km. Consequently, the density increased in a log-linear fashion from the study area edge inwards, having a plateau at distances ≥5 km from the edge. Thus, inside the core we obtained a constant density, whereas in the edge area it declined towards the edge.

Magnitude of density – Previous research has compared the performance of SCR models under different density levels (e.g., Sollmann *et al.*, 2012, Sun *et al.*, 2014, Wilton *et al.*, 2014). However, the density and abundance values evaluated were seldom as low as those reported for certain species, such as

Leopard in Southeast Asia (Chapter 3). Importantly, recent studies showed that although SCR models were amenable to use with a variety of spatial designs, bias and precision were affected when data were sparse (Clark, 2019, Wilton *et al.*, 2014). Therefore, to mimic scenarios typically encountered for Leopard and other large carnivores in Southeast Asia, we considered two low-density population scenarios, which were based on the low and high end of densities obtained for Leopard in the wider region (Chapter 3). Specifically, we simulated data sets using population sizes of N_{VLD} = 5 and N_{MLD} = 30 within the 1,024 km^2 simulated area, corresponding to densities of about 0.5 individuals/100 km^2 and 3 individuals/100 km^2, respectively.

Sampling design scenarios – Most research, both empirical and simulation-based, has focused on regular or uniform grids, in which traps are arranged in grids regularly spaced, and where trap spacing represents the main design decision: detectors arranged closer together result in a larger number of spatial recaptures of fewer individuals (maximising for spatial recaptures), whereas spreading out the detectors results in larger number of individuals but fewer spatial recaptures (maximising for captures; Dupont *et al.*, 2020, Sun *et al.*, 2014). Clusters, on the other hand, have been suggested as an alternative that can outperform regular arrays by allowing for more area to be covered, thus increasing numbers of unique individuals detected, while simultaneously increasing the number of spatial recaptures (Sun *et al.*, 2014). However, the use of a cluster configuration design also requires structural decisions, such as the number of stations per cluster, and the spacing within and among clusters, which may yield results worse than expected based on the decisions made (Clark, 2019). Therefore, because the idea of optimal sampling design for SCR remains poorly understood, we placed the camera-trap stations over the landscape following those two main configurations: 1) a regular or uniform layout, and 2) a multi-cluster layout (with 2 x 2 stations per cluster).

Given that most studies are limited by the number of available camera traps, we considered arrays of 49 or 81 camera-trap stations (each station consisting of a pair of camera traps), which are typical of most studies in Southeast Asia (Chapter 3, Hedges *et al.*, 2015, Ngoprasert *et al.*, 2017, Rostro-

García *et al.*, 2018, Simcharoen and Duangchantrasiri, 2008). Specifically, based on the number of available stations, we simulated 7x7 and 9x9 regular square arrays, and 4x4 and 5x5 multi-cluster arrays (Figure 4.1). Because previous studies in the region have reported the loss of camera-trap stations, mostly due to theft by humans (Chapter 3), each data set had around 5% of the stations randomly removed to better emulate field conditions, reducing the nominal trapping grid to 46 and 77 camera-trap stations, respectively. For each simulated data set station locations were newly drawn. In addition, for each kind of array we evaluated SCR performance considering two distances commonly used to space camera-trap stations when studying Leopard and similar-size carnivores in Southeast Asia, namely, 2 km and 4 km. For the multi-cluster design, these distances were used to space stations within a cluster (i.e., intra-cluster spacing), with the spacing between clusters (i.e., inter-cluster spacing) varying based on the number of available stations. Because in reality stations are seldom placed at the exact planned locations (i.e., forming a perfect grid), we also tested the effects of using different spatial noise levels when placing the stations (i.e., by adding random noise using R's 'Jitter' function with levels 0 and 2, hereafter referred to as jittering), which resulted in some displacement relative to the nominal location. In total, we evaluated 48 scenarios considering different density patterns (homogeneous and heterogenous), trap configuration (uniform and multi-cluster), number of stations (46 and 77), spacing of stations (2 km and 4 km), and spatial noise (i.e., level 0 and 2), of which 24 considered a very low-density population (N_{VLD} = 5) and 24 a moderately low-density population (N_{MLD} = 30).

We simulated encounter histories under a binomial encounter process model by assuming proximity detectors (i.e., devices that do not physically catch but detect the animal), in which individuals are detected at most once in each trap during each sampling occasion (Royle *et al.*, 2014). We used a half-normal detection function, which is defined by two parameters: the baseline encounter probability parameter (p_0), or the probability of detecting an individual at the activity centre, and the spatial scale parameter (σ) that describes the decline in probability of detection with distance from the activity centre (Efford and Fewster, 2013, Royle *et al.*, 2014). Designs were generated using fixed values of p_0, σ, and number of occasions. Specifically, for all scenarios we used a baseline encounter probability p_0 = 0.01,

based on previous studies of the species in the region (Chapter 3, Hedges *et al.*, 2015, Rostro-García *et al.*, 2018), and simulated trap encounters over 81 effective days, representing a nominal 90-day survey (typical in large carnivore studies to achieve a compromise between approximating a closed population and collecting enough data) with a 10% reduction in length due to camera malfunctioning or lack of batteries. Because density and home range size are often negatively correlated (Efford *et al.*, 2016, Sollmann *et al.*, 2012), we selected two different values of σ to correspond to the selected values of N, such that a decrease in density was associated with an increase in σ (i.e., $N_{VLD} = 5$, $\sigma_{VLD} = 5$ units, and $N_{MLD} = 30$, $\sigma_{MLD} = 2.5$ units).

Scenario evaluation – For each scenario, we simulated and analysed 100 data sets. Each of the simulated data sets was analysed using SCR models with constant parameters (i.e., SCR0; Royle *et al.*, 2014) implemented in a Bayesian framework using JAGS (Plummer, 2003) accessed through R ver. 3.6.1 (R Core Team, 2019) using the R package jagsUI ver. 1.5.1 (Kellner, 2019). We ran three parallel Markov chains with 6,000 iterations each, of which we discarded the first 3,000 as burn-in. For each parameter we assessed chain convergence using the Gelman-Rubin statistic, assuming that values $\hat{R} < 1.1$ indicated convergence (Gelman *et al.*, 2004), and visually inspected the time series plots. All estimates of N $(\widehat{N})$ were compared to the truth in the data simulation, and estimated means, standard deviations, relative root mean square error (RRMSE), percent relative bias (%RB), coefficient of variation (CV), and coverage (i.e., the proportion of 95% Bayesian credible intervals that included the true parameter value), were used to evaluate model performance and the effects of the different scenarios. We considered CV < 20%, RRMSE < 25%, and %RB < 10% as desired levels of precision, accuracy, and bias, respectively.

4.3.2 Empirical data: Leopard in Southeast Asia

We studied Leopard using systematic camera-trapping surveys in two important low-density populations of Southeast Asia (Chapter 2 and Chapter 3), one in Cambodia and one in Thailand (details below). Both study sites were surveyed for approximately 3 months, during their respective 6-month dry seasons. In

general, each station consisted of a pair of camera traps operating 24 hours/day, which were placed on opposite sides of a trail to obtain photos of both flanks of each detected individual, and thus allow for individual identification. Cameras were placed on trees located 1.5-5 m from the middle of the trail, and motion detectors set to trigger at a height of 40-45 cm above the centre of the trail. When possible, stations were checked approximately one month after setting. During these checks, some stations were relocated to nearby locations to reduce risk of theft, flood, or fire.

Cambodia

The first case study was conducted in Srepok Wildlife Sanctuary (hereafter Srepok; 3,730 km^2), formerly known as Mondulkiri Protection Forest, located in the Eastern Plains Landscape (EPL) of Cambodia. The EPL appears to hold the only viable population of all of Cambodia, Laos, and Vietnam (Rostro-García *et al.*, 2016a, Rostro-García *et al.*, 2019), and the last remaining Leopard population of Southeast Asia inhabiting a landscape dominated by open dry deciduous forests (Rostro-García *et al.*, 2016a). Srepok is the largest protected area in the EPL, and is dominated by open and dry deciduous dipterocarp forests (ca. 70% of the site) interspersed with small patches of closed evergreen forests (Rostro-García *et al.*, 2021). We originally set 200 camera-trap stations spaced 2-3 km throughout the core zone during 2018, several of which were stolen or damaged; thus, 163 camera-trap stations were operational throughout the survey.

Thailand

The second case study was conducted in Salakpra Wildlife Sanctuary (hereafter Salakpra; 868 km^2), the first wildlife sanctuary of the country, located in Kanchanaburi Province. Salakpra is part of the Western Forest Complex (WEFCOM), which together with the adjacent Southern Forest Complex in Myanmar, comprise the Northern Tenasserim Forest Complex, the largest remaining forest track in mainland Southeast Asia, and one of the two remaining strongholds for the Indochinese Leopard (Rostro-García *et al.*, 2016a). Salakpra consists of mixed deciduous and dry dipterocarp forests, and contains a

population of both spotted and melanistic Leopard. During 2017, we set 87 camera-trap stations spaced 2 km apart in the core zone and 4 km apart in the rest of the park. Cameras at 3 stations were damaged by elephants or stolen; thus, 84 stations were operational throughout the survey.

Analysis

Density estimates were obtained using SCR models implemented in a Bayesian framework. The state-space was created by buffering each of the camera-trapping grids by at least 4σ, using a discrete set of equally spaced points, representing possible Leopard activity centres (Royle *et al.*, 2009a, Royle *et al.*, 2009b). Because the Leopard is a habitat generalist and the core areas where the surveys were conducted were mostly surrounded by forested areas, we considered the buffer area as suitable habitat, and only excluded regions from the state-space that were distinctly non-habitat (e.g., large lakes). Although accounting for differences in movement and detection probability between sexes improves density estimates in felids (Sollmann *et al.*, 2011), we limited the complexity of the models (i.e., we used SCR0 models; Royle *et al.*, 2014) due to the sparsity of the data.

Effects of reduced number of camera traps using empirical data

To study the effect of a reduction in effort while still sampling the same sized area on the parameter estimates, we conducted 'data dilution' simulations with the empirical data. Specifically, we simulated a reduction in available camera-trap stations by randomly removing a percentage of the stations and performed model fitting only with data from the remaining stations. For each case study, we randomly removed stations in 10% increments, until the lower bound of stations used by previous studies in the region was reached (i.e., 15-20 stations; Ngoprasert and Gale, 2019, Rayan and Mohamad, 2009, Sunarto *et al.*, 2013), with 100 simulation replicates per dilution level. For each parameter we assessed chain convergence using the Gelman-Rubin statistic, assuming that values $\hat{R} < 1.1$ indicated convergence (Gelman *et al.*, 2004), and visually inspected the time series plots. We present the density estimates and

used the full data set as reference for comparisons among dilution scenarios. We considered %RB <15% as adequate.

4.4 Results

4.4.1 Simulation study

Very low-density population

For the very low-density (VLD) scenarios (N_{VLD} = 5, σ_{VLD} = 5), the main differences in precision (CV), accuracy (RRMSE), and bias (%RB) of the estimates of abundance *N* obtained were due to the number, layout and spacing between stations (Figure 4.3, Table 4.1). No discernible difference in the results was generated by jittering the stations, compared to no jittering. In addition, an edge effect in density in general had little influence on the estimates. Unsurprisingly, a larger number of stations resulted in less biased and more precise estimates than when a smaller number of stations was deployed (Table 4.1). In addition, estimates improved when stations were spaced farther apart (i.e., 4 km) than when they were set closer together (i.e., 2 km), independently of the number of stations used. Overall, performance deteriorated when a smaller spacing between stations was utilized (Table 4.1). The worse performance corresponded to the scenarios where fewer stations and smaller spacing was used, particularly under a uniform grid for which the most biased (%RB: 17.27; Sc. 3 - Table 4.1) and least accurate (RRMSE: 0.39; Sc. 1 - Table 4.1) estimates were obtained. In such cases, the use of a multi-cluster layout resulted in better estimates (%RB: 4.26-4.46, RRMSE: 0.14-0.16). In contrast, with a larger spacing between stations, the uniform grid covered most of the study area and provided good estimates. Even when fewer stations were used, the uniform grid provided less biased (%RB: 0.63; Sc. 7 - Table 4.1) and more accurate (RRMSE: 0.07; Sc. 9 - Table 4.1) estimates when a larger spacing between stations was used. With a multi-cluster layout, a smaller number of stations resulted in gaps in the middle of the array, whereas when the number of stations was increased the spacing between them decreased, essentially generating a mix of 3 km and 4 km between stations, corresponding to the inter- and intra-cluster spacing, respectively (Figure 4.1). Except for 3 of the evaluated cases (Sc. 1, 3, and 5 - Table 4.1), all of which

considered fewer traps closer together under a regular layout, we obtained robust estimates with the desired levels of precision (CV < 20%), accuracy (RRMSE < 25%) and bias (%RB < 10%). Notably, in the majority of scenarios estimates of *N* were greater than 5 and thus positively biased (Table 4.1).

Moderately low-density population

Under the moderately low-density (MLD) scenarios (N_{MLD} = 30, σ_{MLD} = 2.5), there were 3 simulated data sets that had no spatial recaptures (i.e., no animals were captured in more than one location), producing unusable data in 1% of the replicates (Sc. 30, 32, and 34 - Table 4.1). As with the VLD scenarios, in the MLD scenarios a larger number of stations and wider spacing generally resulted in better estimates (Figure 4.4, Table 4.1). In contrast to the VLD scenarios, with the MLD scenarios the use of fewer stations with less spacing led to larger RRMSE and positively biased estimates when using a multi-clustered layout (RRMSE: 0.60-0.63, %RB: 22.62-33.87) compared to a uniform layout (RRMSE: 0.28-0.32, %RB: -0.89-16.69; Table 4.1). However, the overall performance of multi-cluster layouts improved when the intra-cluster spacing between stations increased. Under the MLD scenarios the performance of the layouts varied based on the edge effect in density considered. When an edge effect in density was present, bias increased for the scenarios considering the smallest spacing and a regular grid, regardless of the number of stations considered (Figure 4.4, Table 4.1). Interestingly, when considering an edge effect and more stations at a smaller spacing, a uniform layout led to larger positive bias compared to a multi-cluster layout (%RB: 16.34 vs 2.67, respectively; Sc. 39 and 40 - Table 4.1). The smallest RRMSE (RRMSE: 0.10) corresponded to the larger number of stations and greater spacing with no edge effect in density (Table 4.1). Overall, both %RB and RRMSE values were larger than those obtained for the VLD scenarios (Figure 4.5). Importantly, for several of the evaluated cases we did not obtain estimates with the desired levels of precision, accuracy, and bias (Table 4.1). As with the VLD scenarios, the majority of the scenarios were positively biased (Table 4.1).

4.4.2 Empirical data

Our simulations using empirical data to investigate the effects of reduced sampling intensity in SCR performance suggested that in general precision decreased and bias (divergence from the estimate based on the full data set) increased with decreasing sampling intensity (i.e., total number of stations). Similarly, the degree of convergence decreased when the number of detectors decreased, while the number of cases that had no spatial recaptures increased. In both cases %RB was adequate (<15%) when ca. ≥ 50 stations were used, corresponding to 30-90% and 60-90% percentage of data used from case study 1 and 2, respectively (Figure 4.6 and 4.7). An increase in dilution, or decrease in the percentage of data used, considerably increased relative bias, particularly when < 20 stations were used.

4.5 Discussion

The number of studies using SCR methods has increased over the last decade and with it the effort and funding invested in surveys that aim to estimate population parameters (Steenweg *et al.*, 2017). Although the developments in SCR methods have increasingly placed camera traps at the forefront of monitoring and conservation programs (Green *et al.*, 2020), camera-trap surveys are no panacea as they can be logistically challenging, costly, time consuming, and physically demanding to implement, particularly when studying low-density populations of large carnivores in remote areas. Thus, improving study design is paramount to appropriately obtain data, study wildlife ecology and conserve species while effectively using the limited conservation resources (Kristensen and Kovach, 2018). Overall, our study corroborates that SCR models generally perform well and are flexible to estimate population parameters across a range of study designs commonly used to survey low-density population of large carnivores. However, while frequently robust to low-density populations and the corresponding sparse data sets (Borchers and Efford, 2008, Royle *et al.*, 2014, Wilton *et al.*, 2014), our results also illustrate that under the scenarios explored, SCR model performance varied based on the magnitude of population density and the sampling design used.

Under the very low-density (VLD) scenarios, for a majority of the cases evaluated, we obtained robust estimates of abundance with the desired levels of precision (CV < 20%), accuracy (RRMSE < 25%) and bias (%RB < 10%). In particular, estimates improved when a larger number of stations was used and when these were spaced farther apart from each other (i.e., 4 km). These results are likely linked to the extremely low density and corresponding value of σ considered: more stations spaced farther apart increased the effective survey area and thus chances of capturing the few individuals; yet, with a σ of 5 km, even at a 4-km spacing, the array still produced spatial recaptures. Consequently, the wider spacing increased sample sizes and information on σ. In contrast, scenarios performed more poorly when fewer stations were used, especially when these were spaced closer together within a uniform grid layout. With fewer stations spaced closer together the effective survey area decreased, which resulted in reduced sample sizes. Along with this reduced spatial coverage, under a uniform layout the stations were mostly concentrated in the centre of the study area, which consequently resulted in several individuals captured only on the edge of the array, thus providing negligible information from which to estimate σ. This was further evidenced if an edge effect in density was considered when using a uniform layout, in which the reduced spatial coverage, and hence non-representative sampling, resulted in a slightly more biased estimate. Noteworthy, when fewer stations spaced closer together were used, incorporating a multi-cluster layout improved the estimates, likely because this approach increased the number of spatial recaptures which resulted in improved estimates of σ. Therefore, our results suggest that in cases where fewer camera traps are available to survey a VLD population, particularly if they have to be spaced closer together (e.g., due to logistical constraints), incorporating clustering into the study design can be advantageous. This is in accordance with previous studies that suggested incorporating clustering can be beneficial for estimating American Black Bear density using hair snares (Clark, 2019, Sun *et al.*, 2014). When stations were spaced farther apart such that most or the entire study area was covered, then a uniform grid represented a good option as it exposed the few individuals, which had relatively large σ, to sampling, suggesting this layout can be advantageous when a majority of the study site can be covered.

This practical alternative also safeguards from losing several spatial recaptures in real-life implementations where σ is unknown and might be smaller than expected.

Results under the moderately low-density (MLD) scenarios differed from those obtained under VLD scenarios, partly due to the increased number of individuals and partly due to the smaller value of σ. Particularly, a σ of 2.5 km implies that in the MLD scenarios, stations were more widely spaced relative to both σ (e.g., a 4 km spacing is now 1.6σ instead of 0.8σ as with the VLD scenarios), and the edge effect (i.e., 5 km edge effect in density is now equivalent to 2σ in width). In addition, because p_0 was the same in VLD and MLD scenarios, and overall detectability is a function of p_0 and σ, individuals in the MLD scenarios had a lower overall detectability. With the larger number of individuals in the MLD scenarios, the influence of the edge effect was more discernible (i.e., results in a more heterogeneous distribution of individuals) than under the VLD scenario, where the low number of individuals precluded the impact of the edge effect from being more apparent (i.e., it is harder for an edge effect to manifest when only 5 individuals are distributed across a large landscape). In contrast to the VLD scenarios, in the MLD scenarios with fewer stations spaced closer together, the use of a multi-cluster layout led to less accurate and more positively biased estimates than those obtained under a uniform grid, independently of the density edge effect considered. These discrepancies likely stemmed from the area covered by the stations under the multi-cluster layout, which resulted in larger gaps where the activity centres of several non-detected individuals occurred as well as underestimates of σ, which subsequently resulted in overestimates of population size. Although many individuals were not detected under the uniform grid, likely there was more information available from several recaptures of the detected individuals, which generated the improved estimates. However, when more stations spaced closer together were used and a density edge effect considered, a uniform grid led to a larger positive bias compared to a multi-cluster layout. This may be due to the uniform grid preferentially sampling the high-density core area when stations were spaced closer together, whereas with the multi-cluster layout the stations were distributed over the study area, including the edge, thus also providing information from lower-density areas (i.e., more representative sampling). Importantly, under the MLD scenarios 3

simulated data sets, all using fewer stations arranged in a multi-cluster layout (Table 4.1) had no spatial recaptures, and thus no information to estimate σ, producing unusable data. Although this occurred in only 1% of the replicates within these 3 simulated data sets, it highlights the risk of using such study designs when conducting field surveys. For several (37.5%) of the MLD scenarios, all of which used fewer stations, we obtained estimates that may not be precise enough (i.e., CV > 20%) to monitor population trends through space and time (Green *et al.*, 2020), three times more compared to the VLD scenarios (12.5%). This emphasizes the need to reconsider commonly used study designs when surveying MLD populations of large carnivores with camera traps.

Under both density scenarios, a larger number of stations and greater spacing generally resulted in better estimates, which is in accordance with results from the empirical data. Our simulations using field data to investigate the effects in SCR performance of reduced sampling intensity (i.e., total number of stations) while still surveying the same sized area, suggested that in general precision decreased and bias increased with a decreasing number of stations. A smaller spatial survey effort impacted the amount of data collected, which in turn affected the ability of the model to estimates parameters, especially when ca. <50 stations were used due to the sparsity of the data. This may be particularly relevant for territorial species, such as Leopard, because individuals space themselves across the landscape and may sometimes have little overlap of home ranges; thus, the smaller spatial effort effectively reduces sample sizes. Previous studies reported the number of traps affected the performance of SCR models (Dupont *et al.*, 2020, Sollmann *et al.*, 2012, Sun *et al.*, 2014), with fewer traps resulting in an increase in bias and designs performing poorly. In general, when dealing with large carnivores that often are territorial and have low encounter rates, a small survey area compared to a typical home range size may yield sparse data, in the form of few detected individuals or few spatial recaptures, which in turn can limit the ability of the model to estimate parameters (Royle *et al.*, 2014, Sollmann *et al.*, 2012). Therefore, the study design should strive to expose as many individuals as possible to sampling and gain better resolution of movement to estimate σ by increasing survey area and number of camera traps deployed when possible. Although it may not always be feasible, this is especially important when a study is concerned with monitoring

population changes (Sollmann *et al.*, 2012), as the amount of data impacts the precision of the parameter estimates. In addition, extending the survey area makes the study more representative of the entire site (e.g., by including more habitat heterogeneity) in empirical implementations.

Our results indicated that optimal spacing of stations was dependent on the density of both the individuals and stations within the state-space. Consequently, although SCR studies can provide precise and accurate population estimates, appropriate study design requires an understanding of the behaviour of the target species, including spatial characteristics (e.g., home range sizes). Previous studies have suggested that a trap spacing that is considerably too large relative to animal movement may be problematic in SCR studies as the lack of spatial recaptures may lead to biased and imprecise estimates (Dupont *et al.*, 2020, Sun *et al.*, 2014). Similarly, a small spacing between traps may generate a small sample size when it limits the extent of the trap array, which may lead to imprecise estimates, suggesting there is an optimal trap spacing, particularly in terms of precision (Efford, 2012, Royle *et al.*, 2014). Previous studies have reported this value to commonly range from 1 to 3σ for a half-normal function (Clark, 2019, Efford, 2012, Royle *et al.*, 2014, Royle *et al.*, 2017, Sun *et al.*, 2014). However, based on our results, it is likely that optimal spacing may be less than σ when studying VLD populations of large carnivores with presumably large home range sizes, evidenced by the fact that several scenarios considering a spacing <1σ generated the desired levels of precision and bias. This suggests that a higher intensity of sampling (i.e., larger number of stations per home range) may be beneficial in VLD cases, as noted by previous studies (Efford and Boulanger, 2019, Kristensen and Kovach, 2018). Nonetheless, care should be taken not to compromise the extent of the sampling area (i.e., achieving smaller spacing at the expense of area coverage). Consequently, when the number of stations is limited, we suggest a spacing no smaller than $\sigma/2$ as that often translates to a smaller effective sampling area.

Encouragingly, no discernible difference was generated under the spatial noise levels evaluated, suggesting that placing stations in a perfect grid, a highly unlikely on-the-ground endeavour, may not be necessary to generate adequate population estimates. Although the effects of heterogeneity in density may not be discernible in VLD scenarios, in general the presence of a density edge effect had little

influence on the estimates, supporting previous findings that SCR models are robust to different density patterns (Dupont *et al.*, 2020, Efford and Fewster, 2013, Royle *et al.*, 2014).

Based on our findings, it is likely that some camera-trap studies targeting low-density populations of large carnivores may not be meeting the requirements necessary to produce unbiased population parameter estimates, likely resulting in overestimates of densities that consequently can be counterproductive for the conservation of the target species. While previous studies have provided recommendations for improving density estimates of large carnivores (Sollmann *et al.*, 2011, Tobler and Powell, 2013), further research on optimal camera-trap design is required, particularly with regards to formalizing an approach to study design. Nonetheless, several design-related issues can be addressed with pilot studies and scenario analysis through *a priori* simulation evaluation of the designs. This approach would allow to evaluate the performance of specific study designs (i.e., their ability to generate useful estimates) before being implemented in the field, and recognize pathologies while conducting surveys allowing for the intervention and resolution of issues before rendering useless data (Royle *et al.*, 2014). Although conducting simulations can be time consuming, computer intensive (multiple replicates for inference), and require technical expertise, recent developments (e.g., *secrdesign* app; Efford and Boulanger, 2019) facilitate the evaluation of different study designs by researchers of all levels of statistical proficiency, and with different resources and time availability. In addition, other alternatives to simulation studies recently have been developed, including computing expected number of detected individuals and of recapture events under different study designs. These approaches, accessible through freely available software (e.g., Durbach *et al.*, 2021, Efford and Boulanger, 2019), allow for fast comparisons among candidate study designs at a low computational cost.

4.5.1 Study limitations and future research considerations

The simulations we conducted were general and based on a limited number of scenarios; thus, there is scope for further refinement. For instance, the designs we evaluated, both under uniform and multi-cluster layout, followed a regular spatial pattern (i.e., same spacing) of the stations. However, an irregular

spatial structure (i.e., different spacing between stations) could have resulted in an improved resolution of the movement distances and thus in better estimates of σ (Dupont *et al.*, 2020). Similarly, we based our simulations on a fixed-square study area, but this may not be representative of challenges encountered when surveying irregular areas in practice. Additionally, a regular area might be problematic when home ranges of the target species are asymmetrical and oriented perpendicular to the grid (Efford, 2019a); neither of which were considered on our simulations. Furthermore, we defined the number of camera traps to use based on the number of stations frequently deployed in camera-trap studies, and considering limitations likely to be encountered by researchers, including the upper bound of available camera traps. Therefore, we did not explore other camera-trap configurations (e.g., 3x3 or 4x4 multi-cluster layouts), which could have provided better population parameter estimates (Clark, 2019). Although these considerations may be relevant for certain cases (e.g., irregular study areas), our aim was to investigate the overall performance of SCR models when studying low-density populations using common study designs, instead of optimising the designs and providing the most appropriate solution. We consider that design optimisation is study-specific and needs to be adapted not only to the ecology of the target species, but also to the resource availability and logistical feasibility of the study. In such cases where a design optimisation is sought, recently developed alternatives (e.g., Durbach *et al.*, 2021, Dupont *et al.*, 2020, Efford and Boulanger, 2019) allow the generation of customised and improved near-optimal sampling study designs, not only for single species but also for the study of ecological communities through multi-species sampling framework. Analogously, while the number of individuals considered under the VLD scenarios may not have been enough to discern the impact of an edge effect in density, our aim was to investigate the performance of SCR models when considering empirically based low population sizes, which are becoming increasingly prevalent in defaunated areas, such as Southeast Asia mainland.

Importantly, our simulations were generated using a fixed value of baseline encounter probability (p_0) to limit the number of scenarios to be explored; nonetheless, results under MLD scenarios may have improved if a higher p_0 was used to compensate for the reduced per-individual data

due to the lower value of σ. In addition, although unmodelled heterogeneity (e.g., differences in detectability that arise from intrasexual or other differences in behaviour) can lead to inaccurate population estimates (Sollmann *et al.*, 2011), we did not account for differences in movement and detection probability between sexes, due to the sparse data sets that characterise low-density populations studies. Not incorporating sex-specific differences in our analyses also allowed for comparisons with previous studies and the empirical data, which were sparse and had skewed sex ratios. Surveys that obtain insufficient data can consider, when possible, aggregating data across ecologically-similar sites in order to account for heterogeneity in detection and improve parameters estimates (Chapter 3, Mohamed *et al.*, 2021, Wilting *et al.*, 2012).

Noteworthy, the edge effect in density that we tested was not meant to be a representation of the phenomenon present on-the-ground but to exemplify an ecologically realistic scenario based on empirical data of the species. It is likely that edge effects in density behave differently and are species- and site-specific. Notably, the impact of a density edge effect may be more discernible under scenarios considering larger population sizes and different survey designs than those considered here. For example, when fewer camera traps spaced closer together were used, the grid layouts that we considered had different degrees of representativeness of the study area, which in turn could have influenced the results towards area representativeness rather than spatial arrangement of the traps. Further research is required to better understand and represent spatially variant density patterns of animal populations.

When individuals can be uniquely identified by their natural markings, as is the case with most large felids, camera traps are typically set in pairs to simultaneously record both sides because each side of an individual has different markings. However, when the number of cameras is limited, the individuals are well known, or it is logistically more feasible (e.g., due to difficult terrain), setting single cameras can be preferable to paired cameras as it optimises the use of scare resources by allowing more locations to be sampled. Consequently, we suggest further investigation of SCR models performance considering single cameras, as incorporating such strategy can be advantageous particularly for studies with limited resources in well-studied areas. Recent advances (e.g., spatial partial identity models or SPIMs) allow

for partial identity samples (i.e., individuals whose identity is only known from a single flank) to be used in the analysis by using the spatial location where these samples are captured to probabilistically resolve their complete identities (Augustine *et al.*, 2018). These advances permit the deviation from standard camera-trap survey designs, and the generation of more flexible designs that can be tailored to survey-specific considerations.

4.5.2 Implications and recommendations

Overall, we found that while some design recommendations from prior SCR studies were appropriate, others were not applicable to low-density populations of Leopard. The same is likely true for low-density populations of other large felid species, notably Tiger (*Panthera tigris*) and Jaguar, which are the other two more commonly studied species using camera traps (Green *et al.*, 2020). Importantly, our findings highlight the relevance of devising appropriate study designs for the target species. Broad recommendations have been made about how to conduct camera-trap surveys, which have been used by several studies without study-specific modifications, likely resulting in estimates that may not be sufficiently precise. In accordance, a recent review of SCR studies using camera traps found that a majority produced density estimates that may not be precise enough for long-term monitoring of the populations (Green *et al.*, 2020). This in turn can be counterproductive to the conservation of species, and must be addressed to better conserve remaining populations of large carnivores.

Often the study design generation assumes that researchers have access to data on the approximate values of SCR parameters of the species in the study area; however, for certain species and regions this is seldom the case (e.g., Leopard in Southeast Asia). This precludes researchers from using appropriate parameter values (e.g., σ) to follow previous design recommendations (e.g., trap spacing of 2σ). Consequently, researchers tend to adopt design strategies used in previous surveys, which may not be appropriate for the spatial behaviour of the target species at their site. In addition, arbitrary decisions often are made, which may lead to protocols that provide worse than expected data collection. Because, as evidenced in our results, data and survey designs from previous studies targeting different species or

study areas can be inadequate for effective estimation, we suggest that, when possible, pilot studies should be conducted. Pilot studies also provide a realistic way to estimate the monitoring efforts (e.g., numbers and maintenance of cameras) required to study the target species and achieve the desired precision, as well as familiarity with the equipment and field conditions. These studies, together with simulations, can provide relevant information and guide data collection by evaluating performance and optimising efficiencies, important for the often expensive and time-consuming surveys typical of low-density populations of large carnivores. In addition, we suggest incorporating complementary information derived from other sources, such as telemetry studies or DNA sampling, when available as this has been shown to increase the precision of the population parameter estimates (Paterson *et al.*, 2019).

Due to the flexibility of SCR models, a wide variety of modifications for particular sampling situations has been developed. This, together with the practicality and wide adoption of camera traps to study otherwise elusive species, as well as the ever-increasing technological developments, likely will result in constant improvements in the analytical approaches to obtain camera-trap data. With these improvements should come a parallel evaluation of their performance to ensure that estimates are precise. This is especially critical when studying low-density populations of large carnivores, given the exceptional importance they play in ecosystems and their concerning conservation status. If population parameter estimation is unlikely to be possible, then other avenues, such as habitat use, are available to provide valuable information of the target species, which can be crucial for their conservation in a rapidly changing world.

In developing sampling designs for SCR studies of low-density populations of large carnivores, we suggest the following considerations in addition to survey-specific strategies for devising an appropriate design for the target species:

1) Collect ecological data of the target species from the study area (e.g., σ, p_0, home range size). If such information is not available, and time and resources allow, conduct a pilot study considering a spacing of 1-3σ, obtaining the value of σ from studies of the same or similar species in comparable ecological

circumstances. When movement is data is available, the value of σ can be derived using estimates of 95% use areas of bivariate normal home ranges ($A_{.95}$) according to:

$$\sigma = \sqrt{\frac{A_{.95}}{\pi \cdot (2.45)^2}}$$

2) Determine the extent of the study area, number of camera traps available; then, using the information from existing data or extrapolating from the pilot study, conduct simulations (custom-written or from existing software) or compute alternatives such as the expected number of individuals and of recaptures (e.g., by using freely available software [Efford, 2019b, 2019c]). Consider a spacing 1-3σ and a trapping grid with an extent larger than (or at least as large as) the average home range of the species. Importantly, the selected design should be logistically feasible (e.g., cameras can be set up and maintained given the access to different areas and man-hours). This *a priori* design evaluation is valuable to ensure that large enough samples are obtained to estimate the parameters of interest. We recommend using a minimum of 50 camera-trap stations, but use a larger number of stations when possible, particularly when surveying large study areas. If a multi-cluster layout is considered (e.g., design optimisation renders it the most appropriate sampling strategy), we suggest a minimum of 2x2 clusters for practical reasons (i.e., camera failure in smaller clusters can result in a large impact by essentially eliminating the cluster).

3) Although not explored in detail in this study, the precision of the estimates will increase with a higher detection probability. Therefore, in order to maximise detection probabilities, identify the location of the stations around the potential placement sites by looking for fresh signs (e.g., tracks, urine and scrape markings) or favourable features (e.g., ridges, well-established trails) considering knowledge about the behaviour and range of movement of the target species. Record the location of the station (e.g., on/off road) as this could be incorporated into the model to account for differences in detection probabilities. To improve detection probabilities in low-density population of elusive species, allow the survey to last the maximum number of days whilst considering population closure (e.g., 90 days). We emphasize that these should be species and site-specific considerations.

4.6 Acknowledgements

We thank the government agencies of each country for granting the permits to conduct research in the study areas, as well as the different organisations and field assistants who supported the study. For the work in Cambodia, we would like to thank collaborating organisations, including WWF Cambodia, Ministry of Environment, and Forestry Administration-Ministry of Agriculture, Forestry, and Fisheries (Royal Government of Cambodia), as well as support in the field provided by M. Sarady, and research rangers from Srepok. In Thailand we would like to thank collaborating organisations including ZSL-Thailand, Department of National Parks, Wildlife and Plant Conservation, Faculty of Forestry at Kasetsart University, and Faculty of Veterinary Medicine at Mahidol University, as well as rangers from Salakpra. Funding for field work was provided by Panthera, while SR-G's analyses and writing was supported by a Foley-Béjar Scholarship, provided by Balliol College, University of Oxford, and a grant to DWM from the Turner-Kirk Foundation.

Table 4.1 Summary statistics for spatial capture-recapture parameters across 100 simulation replicates each under 48 scenarios considering the presence or absence of a density edge effect (Edge), different number of camera-trap stations (nTraps), spacing between stations (Spacing), spatial noise level in stations location (Jittering), and camera-trap configuration (Configuration) for very low ($N = 5$) and moderately low ($N = 30$) density population of Leopard (*Panthera pardus*) in a simulated study area of 1,024 km^2. Performance was evaluated considering the average estimate of N (Av.est), coverage (i.e., whether the 95% Bayesian credible intervals included the true parameter value), relative root mean square error (RRMSE), percent relative bias (%RB), and coefficient of variation (CV). N = true number of individuals in the state-space, nobs = mean number of individuals observed, Av.sigma = average movement parameter. Bold indicates estimates where the desired levels of accuracy (RRMSE < 25%), bias (%RB < 10%), or precision (CV < 20%), were not obtained.

Scenario	*N*	Sigma	Edge*	nTraps**	Spacing	Jittering	Configuration	Av.est	nobs	Av.sigma	Coverage	RRMSE	%RB	CV
1	5	5	No	49	2	0	Regular	5.67	4.12	5.17	0.97	**0.39**	**13.33**	**32.80**
2	5	5	No	49	2	0	Cluster	5.22	4.72	5.00	0.98	0.14	4.37	13.17
3	5	5	Yes	49	2	2	Regular	5.86	4.45	5.26	1.00	**0.37**	**17.27**	**27.88**
4	5	5	Yes	49	2	2	Cluster	5.22	4.75	5.21	0.99	0.15	4.46	13.66
5	5	5	No	49	2	2	Regular	5.67	4.19	5.17	0.99	**0.38**	**13.39**	**31.43**
6	5	5	No	49	2	2	Cluster	5.21	4.70	5.03	0.98	0.16	4.26	14.83
7	5	5	No	49	4	0	Regular	5.03	4.83	5.05	0.99	0.09	0.63	9.43
8	5	5	No	49	4	0	Cluster	5.10	4.74	5.06	0.99	0.12	2.02	11.44
9	5	5	Yes	49	4	2	Regular	5.13	4.94	5.13	0.99	0.07	2.55	6.07
10	5	5	Yes	49	4	2	Cluster	5.15	4.82	5.24	1.00	0.11	2.90	10.19
11	5	5	No	49	4	2	Regular	5.08	4.88	5.00	1.00	0.08	1.66	7.64
12	5	5	No	49	4	2	Cluster	5.17	4.78	5.02	0.99	0.13	3.32	12.33
13	5	5	No	81	2	0	Regular	5.11	4.65	5.08	1.00	0.16	2.20	15.24
14	5	5	No	81	2	0	Cluster	5.01	4.95	5.02	1.00	0.04	0.17	4.40
15	5	5	Yes	81	2	2	Regular	5.14	4.78	5.29	0.99	0.11	2.75	10.68
16	5	5	Yes	81	2	2	Cluster	4.98	4.92	5.08	0.96	0.06	-0.44	5.58

17	5	5	No	81	2	2	Regular	5.08	4.62	5.15	1.00	0.15	1.68	14.47
18	5	5	No	81	2	2	Cluster	4.98	4.92	4.98	0.97	0.06	-0.47	5.64
19	5	5	No	81	4	0	Regular	5.02	5.00	4.98	1.00	0.01	0.47	0.57
20	5	5	No	81	4	0	Cluster	5.00	4.95	5.04	0.98	0.05	-0.05	5.17
21	5	5	Yes	81	4	2	Regular	5.00	4.97	5.09	0.99	0.04	-0.05	3.55
22	5	5	Yes	81	4	2	Cluster	5.02	4.97	5.17	0.99	0.04	0.34	3.51
23	5	5	No	81	4	2	Regular	5.00	4.97	5.09	0.98	0.04	0.01	3.58
24	5	5	No	81	4	2	Cluster	5.02	4.97	5.00	0.99	0.03	0.32	3.42
25	30	2.5	No	49	2	0	Regular	30.43	11.30	2.60	0.94	**0.31**	1.43	**30.75**
26	30	2.5	No	49	2	0	Cluster	40.16	15.79	2.31	0.92	**0.63**	**33.87**	**40.19**
27	30	2.5	Yes	49	2	2	Regular	35.01	13.45	2.57	0.92	**0.32**	**16.69**	**23.94**
28	30	2.5	Yes	49	2	2	Cluster	36.78	15.29	2.46	0.88	**0.60**	**22.62**	**45.47**
29	30	2.5	No	49	2	2	Regular	29.73	11.40	2.62	0.92	**0.28**	-0.89	**27.91**
30	30	2.5	No	49	2	2	Cluster	38.83	15.64	2.37	0.95	**0.62**	**29.42**	**42.24**
31	30	2.5	No	49	4	0	Regular	31.97	21.12	2.54	0.96	0.20	6.58	18.10
32	30	2.5	No	49	4	0	Cluster	31.88	18.15	2.47	0.98	0.23	6.25	**20.55**
33	30	2.5	Yes	49	4	2	Regular	31.88	21.77	2.52	0.97	0.18	6.25	16.19
34	30	2.5	Yes	49	4	2	Cluster	30.94	17.43	2.56	0.97	0.23	3.15	**22.47**
35	30	2.5	No	49	4	2	Regular	30.99	20.96	2.56	0.93	0.17	3.30	16.14
36	30	2.5	No	49	4	2	Cluster	31.63	17.53	2.45	0.96	**0.26**	5.42	**24.48**
37	30	2.5	No	81	2	0	Regular	29.73	16.28	2.51	0.93	0.19	-0.90	19.44
38	30	2.5	No	81	2	0	Cluster	31.07	22.99	2.50	0.98	0.12	3.57	11.36
39	30	2.5	Yes	81	2	2	Regular	34.90	19.36	2.52	0.86	0.24	**16.34**	15.06
40	30	2.5	Yes	81	2	2	Cluster	30.80	22.79	2.54	0.96	0.13	2.67	12.56
41	30	2.5	No	81	2	2	Regular	29.21	16.30	2.54	0.96	0.19	-2.63	19.13
42	30	2.5	No	81	2	2	Cluster	30.94	22.75	2.52	0.93	0.15	3.14	14.67
43	30	2.5	No	81	4	0	Regular	30.52	25.10	2.49	0.98	0.10	1.74	10.10
44	30	2.5	No	81	4	0	Cluster	30.50	24.16	2.50	0.96	0.11	1.65	10.66
45	30	2.5	Yes	81	4	2	Regular	30.85	24.84	2.54	0.96	0.12	2.83	11.00
46	30	2.5	Yes	81	4	2	Cluster	30.38	24.17	2.51	0.93	0.12	1.26	11.71
47	30	2.5	No	81	4	2	Regular	31.09	25.20	2.50	0.97	0.12	3.63	10.91

48	30	2.5	No	81	4	2	Cluster	30.50	24.00	2.48	1.00	0.10	1.68	9.64

* Yes = density edge effect extending 5 km which caused a total decline of about 40% on Leopard density from the core to the edge
** nominal number of camera-trap stations, actual number considered 5% of camera-trap stations randomly removed to better emulate field conditions (i.e., 46 and 77 stations)

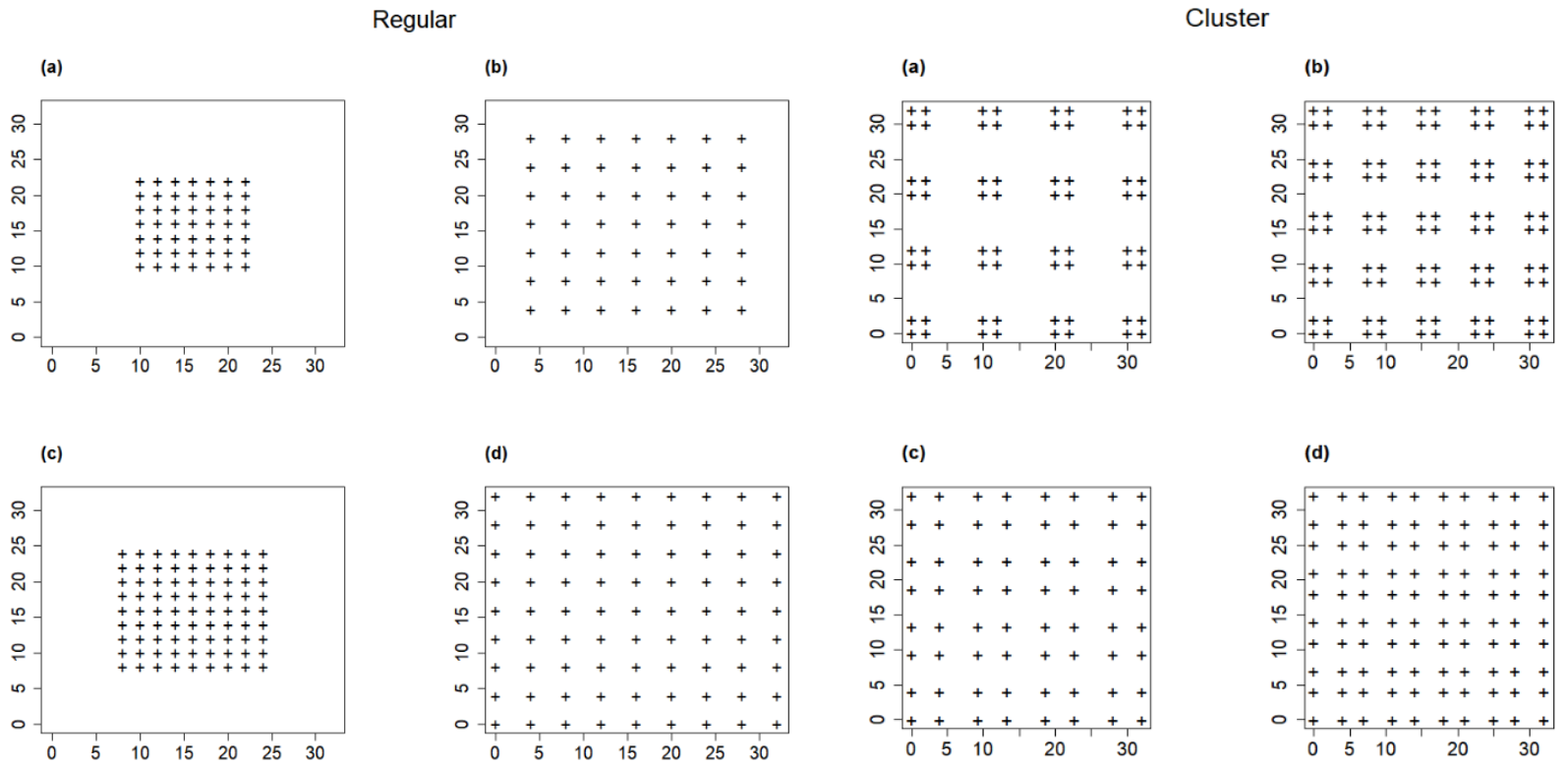
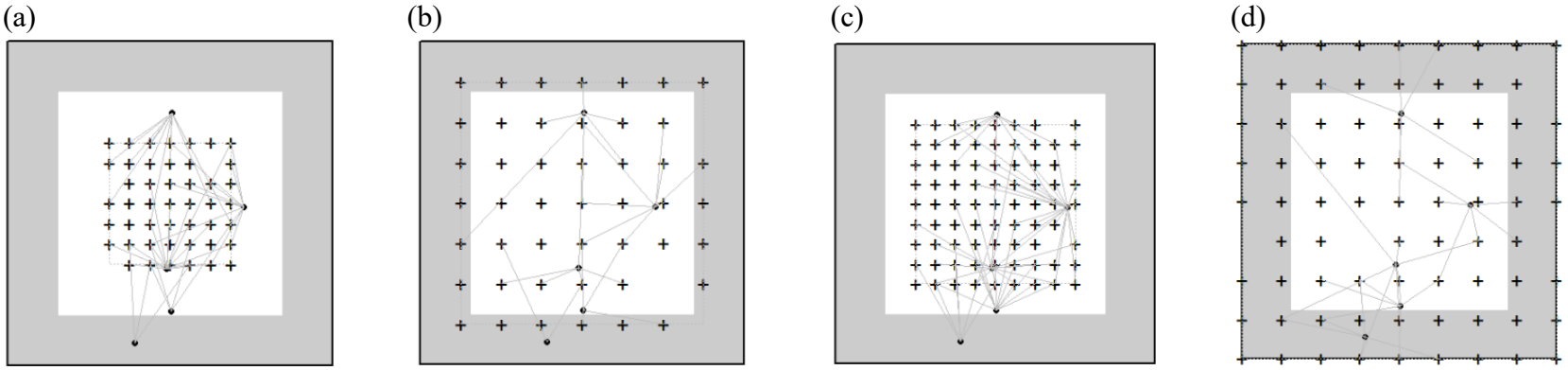


Figure 4.1 Regular and clustered camera-trap station arrangement considered in a simulation study aiming to evaluate the performance of spatial capture-recapture models in estimating density of low-density populations of large carnivores surveyed with camera traps using commonly used study designs: (a) 49 stations, 2 km spacing; (b) 49 stations, 4 km spacing; (c) 81 stations, 2 km spacing; (d) 81 stations, 4 km spacing.

Regular arrays



Cluster arrays

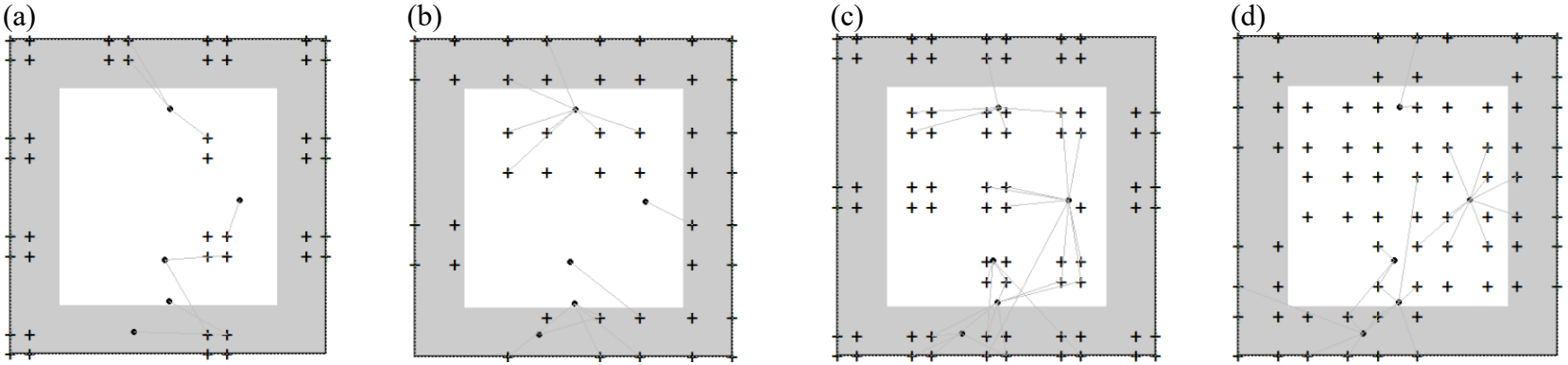


Figure 4.2 Spider plot example representation of 8 camera-trap station layouts considering a population of $N = 5$ Leopard (*Panthera pardus*) with density edge effect, and no jittering considered in a simulation study aiming to evaluate the performance of spatial capture-recapture models in estimating density of low-density populations of large carnivores surveyed with camera traps using commonly used study designs. Two main camera-trap station arrangements were considered, regular and clustered, while varying the number of stations (black crosses) and spacing: (a) 46 stations,

2 km spacing; (b) 46 stations, 4 km spacing; (c) 77 stations, 2 km spacing; (d) 77 stations, 4 km spacing. All stations in which an individual was detected (black circles) are connected through grey lines to the estimated activity centre of the individual. Station locations were newly drawn for each simulated data set.

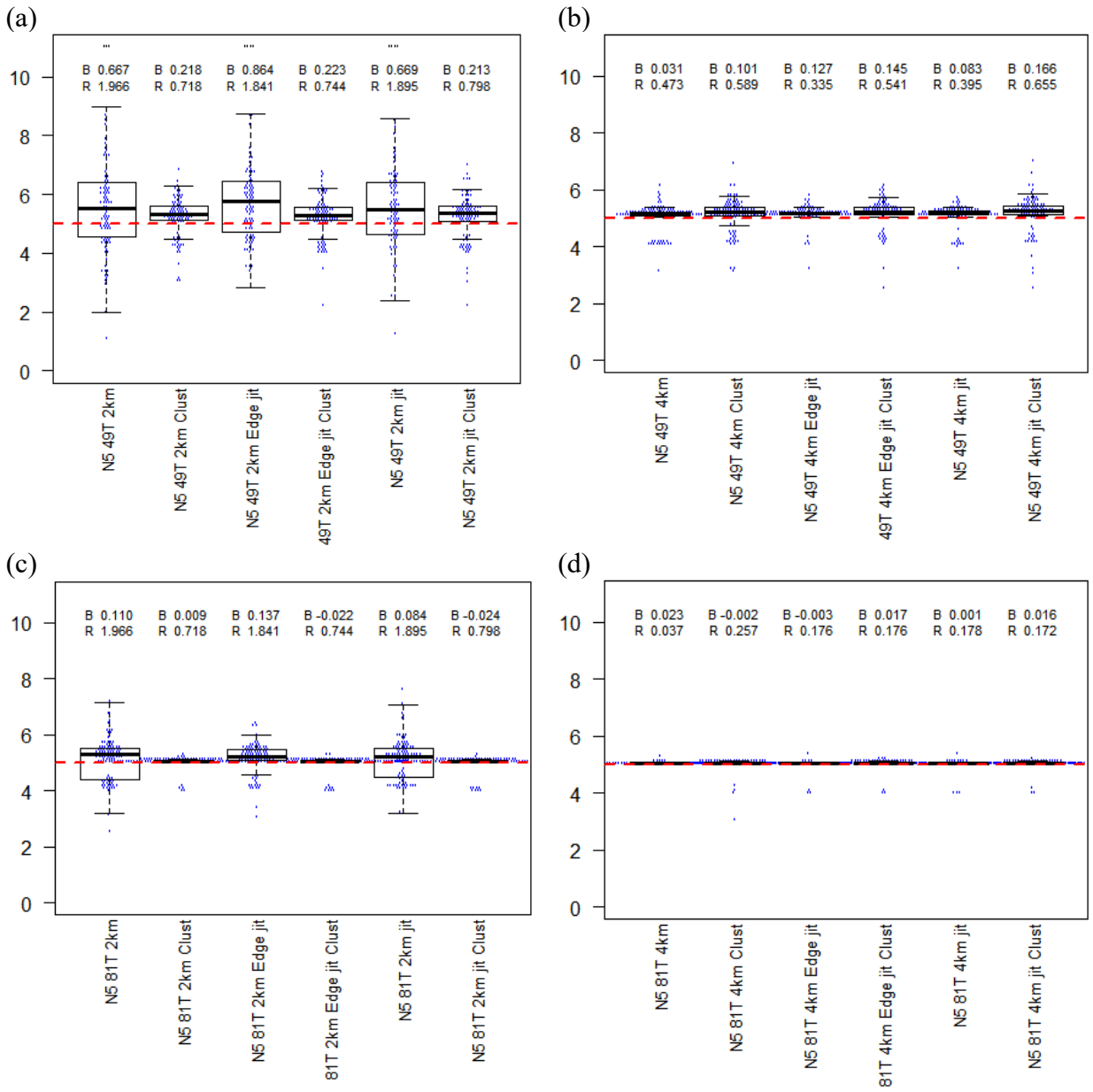


Figure 4.3 Effect on estimates of abundance of using 49 (a, b) and 81 (c, d) camera-trap stations, different station configuration (i.e., regular or cluster), spacing between stations (i.e., 2 km or 4 km), density edge effect (i.e., 0 [no edge effect] and 5 km), and spatial noise level (i.e., 0 [no jittering] and 2) for a very low-density population of $N = 5$ Leopard (*Panthera pardus*) in a simulated study area of 1,024 km^2. For each scenario, 100 data sets were simulated and then analysed using spatially explicit capture-recapture models implemented within a Bayesian framework. Each data set had around 5% of the stations randomly removed,

reducing the nominal trapping grid to 46 and 77 camera-trap stations, respectively. For each simulated data set station locations were newly drawn. The red horizontal line depicts the truth value ($N = 5$). The blue dots indicate the posterior mean estimated for each simulation replicate, and the black dots indicate estimates $N \geq 9$, excluded from the plot for visualization purposes. Estimates of bias (B) and root mean square error (R) are provided for each scenario. Clust = cluster configuration, jit = jittering level 2, Edge = presence of a density edge effect extending 5 km and causing a decline of about 40% in the Leopard density from the core to the edge.

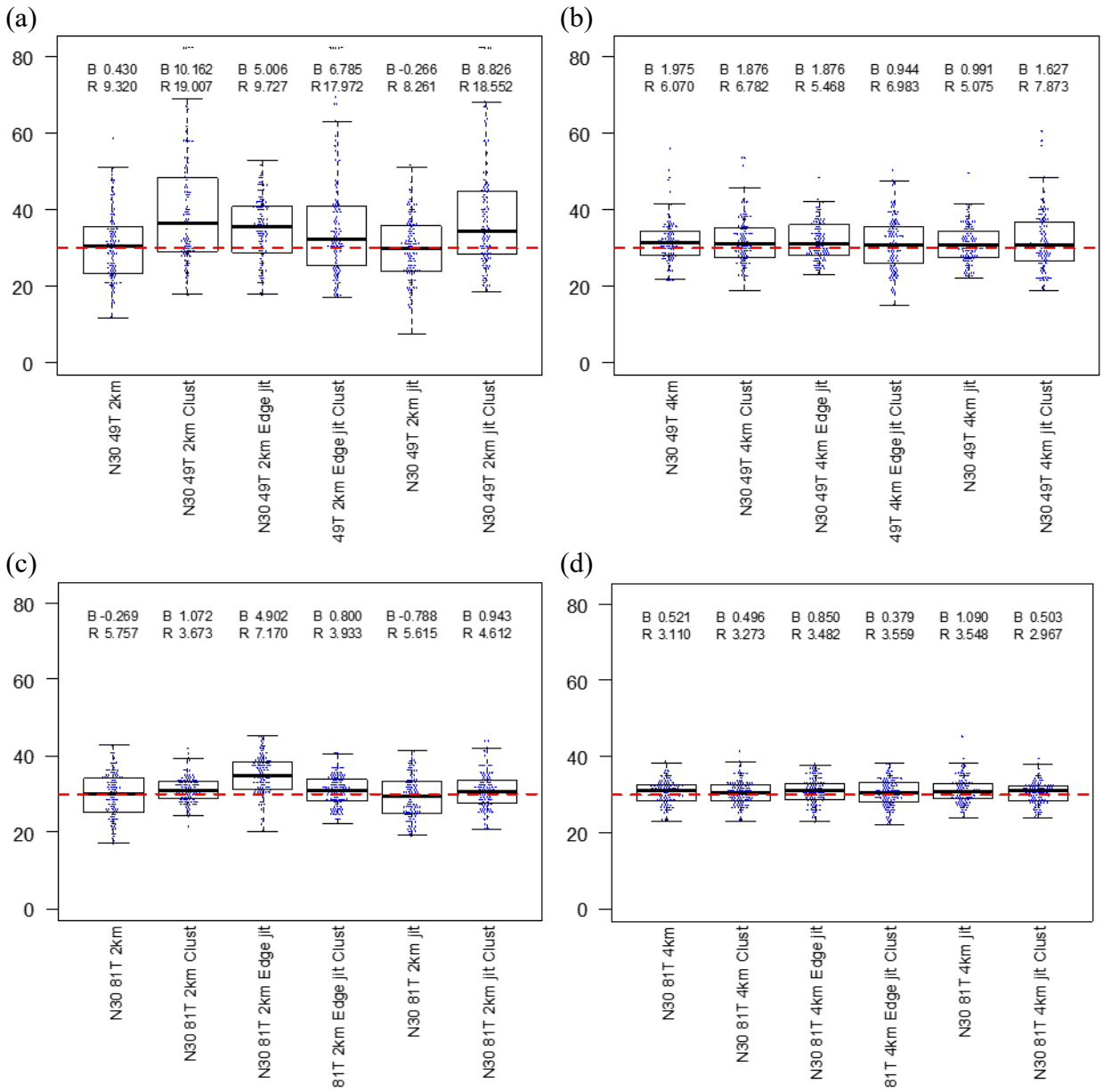


Figure 4.4 Effect on estimates of abundance of using 49 (a, b) and 81 (c, d) camera-trap stations, different station configuration (i.e., regular or cluster), spacing between stations (i.e., 2 km or 4 km), density edge effect (i.e., 0 [no edge effect] and 5 km), and spatial noise level (i.e., 0 [no jittering] and 2) for a moderately low-density population of $N = 30$ Leopard (*Panthera pardus*) in a simulated study area of 1,024 km^2. For each scenario, 100 data sets were simulated and then analysed using spatially explicit capture-recapture models implemented within a Bayesian framework. Each data set had around 5% of the stations randomly

removed, reducing the nominal trapping grid to 46 and 77 camera-trap stations, respectively. For each simulated data set station locations were newly drawn. The red horizontal line depicts the truth value (N = 30). The blue dots indicate the posterior mean estimated for each simulation replicate, and the black dots indicate estimates $N \geq 75$, excluded from the plot for visualization purposes. Estimates of bias (B) and root mean square error (R) are provided for each scenario. Clust = cluster configuration, jit = jittering level 2, Edge = presence of a density edge effect extending 5 km and causing a decline of about 40% in the Leopard density from the core to the edge.

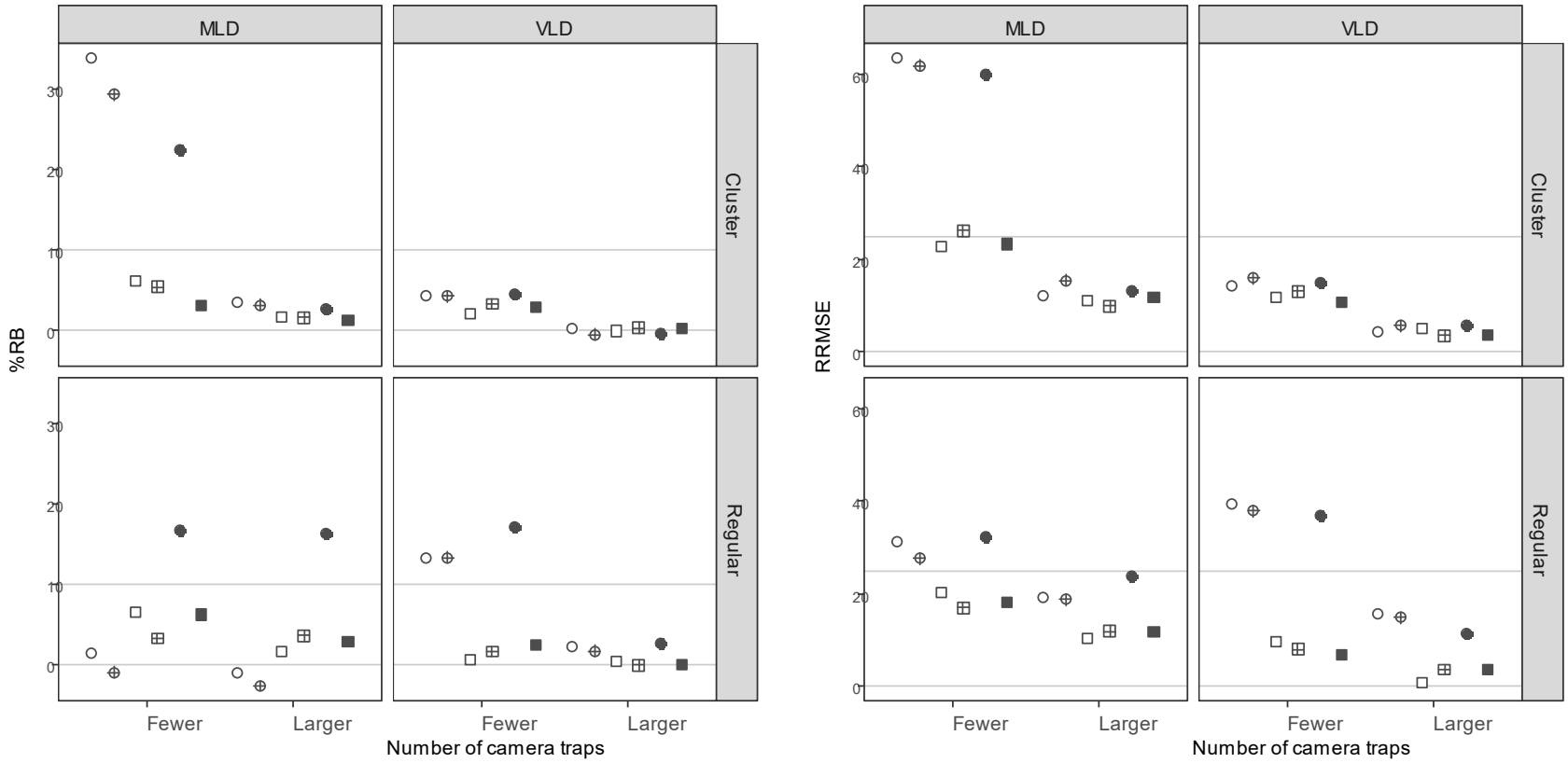


Figure 4.5 Percentage bias (%RB) and relative root mean square error (RRMSE) of estimates of abundance from 48 different scenarios used to evaluate the performance of spatial capture-recapture models when studying low-density populations. The scenarios considered two different Leopard (*Panthera pardus*) density levels (moderately low density [MLD] = about 3 Leopard/100km^2; very low density [VLD] = about 0.5 Leopard /100 km^2), two main spatial density patterns (homogenous = empty shapes, and heterogeneous = filled shapes), different camera-trap station

configurations (regular or uniform and clustered layout), number of stations (fewer = 46, larger = 77), spacing between stations (2 km = circles, 4 km = squares), and spatial noise level (jittering 0 = empty shapes, jittering 2 = cross within shapes).

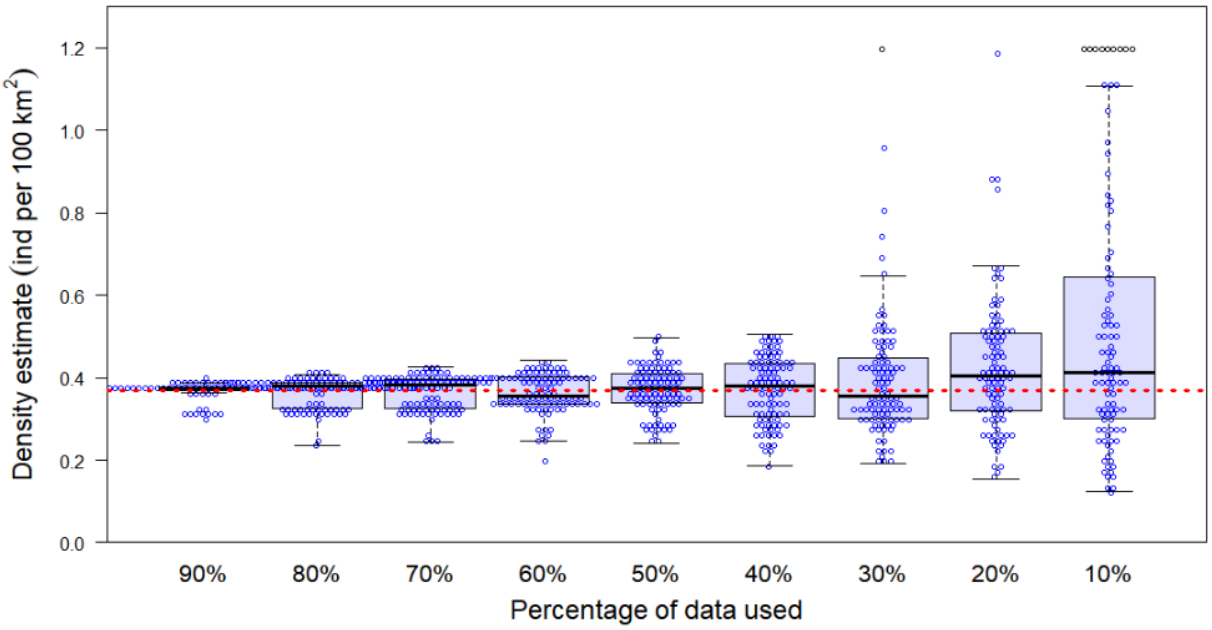


Figure 4.6 Simulation-based assessment of the effects on the posterior mean density estimate of reducing the sample size (total number of camera-trap stations) to 90%-10% from the number used in the field (n = 163) when surveying a low-density population of Leopard (*Panthera pardus*) in Cambodia. For each scenario, 100 data sets were created by randomly drawing a certain proportion of stations from the actual data and the resulting data set analysed using spatially explicit capture-recapture models implemented within a Bayesian framework. The red horizontal line depicts the mean density estimate for the full data set (proportion of data used: 1.0). The black dots indicate $\widehat{D} \geq$ 1.2 Leopard/100 km^2, excluded from the plot for visualization purposes.

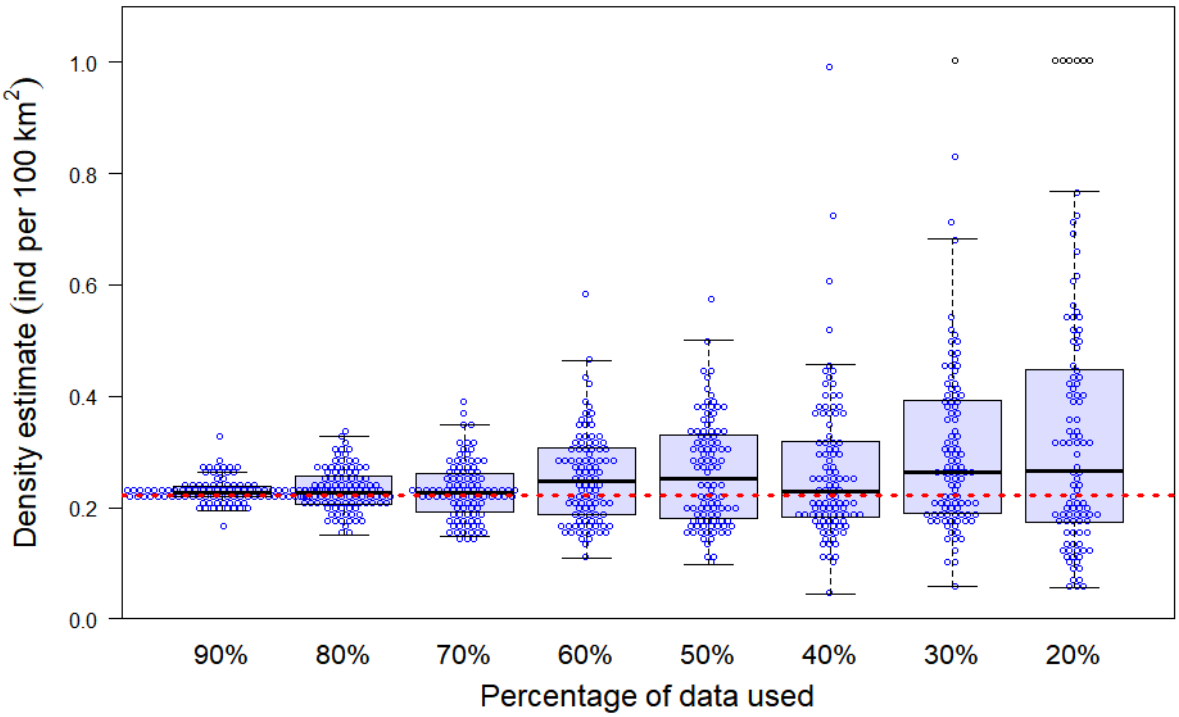


Figure 4.7 Simulation-based assessment of the effects on the posterior mean density estimate of reducing the sample size (total number of camera-trap stations) to 90%-20% from the number used in the field (n = 84) when surveying a low-density population of Leopard (*Panthera pardus*) in Thailand. For each scenario, 100 data sets were created by randomly drawing a certain proportion of stations from the actual data and the resulting data set analysed using spatially explicit capture-recapture models implemented within a Bayesian framework. The red horizontal line depicts the mean density estimate for the full data set (proportion of data used: 1.0). The black dots indicate $\widehat{D} \geq$ 1.0 Leopard/100 km^2, excluded from the plot for visualization purposes.

CHAPTER 5

An adaptable but threatened big cat: density, diet, and prey selection of the Indochinese Leopard (*Panthera pardus delacouri*) in eastern Cambodia

5.1 Abstract

We studied the Indochinese Leopard (*Panthera pardus delacouri*) in eastern Cambodia, in one of the few potentially remaining viable populations in Southeast Asia. The aims were to determine the: (i) current Leopard density in Srepok Wildlife Sanctuary (SWS), and (ii) diet, prey selection and predation impact of Leopard in SWS. The density, estimated using spatially explicit capture–recapture models, was 1.0 Leopard/100 km^2, 72% lower than an estimate from 2009 at the same site, and one of the lowest densities ever reported in Asia. Dietary analysis of 73 DNA confirmed scats showed Leopard consumed 13 prey species, although ungulates comprised 87% of the biomass consumed (BC). The overall main prey (42% BC) was Banteng (*Bos javanicus*), making this the only known Leopard population whose main prey had adult weight >500 kg. Consumption of Wild Pig (*Sus scrofa*) was also one of the highest ever reported (22% BC), indicating Leopard consistently predated on ungulates with some of the largest adult weights in SWS. There were important differences in diet and prey selection between sexes, as males consumed mostly Banteng (62% BC) in proportion to availability, but few Muntjac (*Muntiacus vaginalis*; 7% BC), whereas females selectively consumed Muntjac (56% BC) and avoided Banteng (less than 1% BC). Predation impact was low (0.5-3.2% of populations) for the 3 ungulate species consumed. We conclude that the Indochinese Leopard is an important apex predator in SWS, but this unique population is declining at an alarming rate and will soon be eradicated unless effective protection is provided.

Keywords: *Bos javanicus*, food habits, intersexual differences, *Panthera pardus*, population decline, spatially explicit capture-recapture models.

5.2 Introduction

The Leopard (*Panthera pardus*) has the widest distribution of any felid species, owing to its ability to inhabit diverse habitats ranging from tropical forests and savannahs, to deserts and boreal forests (Stein and Hayssen, 2013). The Leopard also has the broadest diet of all felids, and of all large carnivores, ranging in size from insects to Giraffe (*Giraffa* spp.; Hayward *et al.*, 2006). Despite its adaptability in habitat use and diet, the Leopard has experienced severe declines in distribution and numbers, occupying only 25-37% of its historical range (Jacobson *et al.*, 2016), which led to its recent uplisting to Vulnerable by the IUCN (Stein and Hayssen, 2013). The primary reasons for the decline are habitat loss, prey declines, conflict with humans, and poaching for the wildlife trade, with the relative importance of these factors varying among regions (Jacobson *et al.*, 2016, Stein and Hayssen, 2013). Consequently, the Leopard now occurs in mostly small and fragmented populations, especially in Asia where 7 of 8 subspecies are either already listed, or are being petitioned to be listed, as Endangered or Critically Endangered (Jacobson *et al.*, 2016, Laguardia *et al.*, 2017, Rostro-García *et al.*, 2016a).

The Indochinese Leopard (*P. pardus delacouri*) is a genetically distinct subspecies (Miththapala *et al.*, 1996, Sugimoto *et al.*, 2014, Uphyrkina *et al.*, 2001) that historically occurred throughout all mainland Southeast Asian countries and southeastern China. However, a recent review showed the Indochinese Leopard likely now occurs only in 6.2% of its historical range (Rostro-García *et al.*, 2016a). The Indochinese 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 (Rostro-García *et al.*, 2016a). Rostro-García *et al.* (2016a) identified 3 priority sites and strongholds for Leopard conservation in Southeast Asia: (i) the Northern Tenasserim Forest Complex on the Thailand-Myanmar border, (ii) Peninsular Malaysia, and (iii) eastern Cambodia.

In Cambodia, the Indochinese Leopard has declined dramatically, and now occurs only in 8% of its historical range in the country (Rostro-García *et al.*, 2016a). The only potentially viable population remaining in the country occurs in the Eastern Plains Landscape (EPL; Rostro-García *et al.*, 2016a), a large protected-area complex covering >10,000 km^2 in eastern Cambodia (Gray and

Prum, 2012). In contrast to most of Southeast Asia, the EPL is dominated by savannah-like habitat (i.e., dry open deciduous forests), and is unique for containing the last remaining population of pure spotted Leopard in Southeast Asia (all other Leopard populations in Southeast Asia appear to contain only melanistic Leopard, or a mixture of melanistic and spotted Leopard; Rostro-García *et al.*, 2016a). In 2009, the Leopard density within one protected area of the EPL, Srepok Wildlife Sanctuary (SWS), was estimated to be 3.6 Leopard/100 km^2 (Gray and Prum, 2012), indicating this landscape likely contained a relatively high Leopard population. However, increased levels of poaching that have led to rapid declines of Tiger (*Panthera tigris*) and Leopard populations throughout Southeast Asia (Gray *et al.*, 2017, Lynam, 2010, Rostro-García *et al.*, 2016a, Walston *et al.*, 2010) might have led to a decline of the Leopard population in EPL, although the extent of the possible decline is unknown.

The EPL is known for its high biodiversity, and for having the world's largest population of Endangered Banteng (*Bos javanicus*; Gray *et al.*, 2012a), as well as populations of several other threatened ungulate species, such as Eld's Deer (*Rucervus eldii*; Gray *et al.*, 2012b). The EPL also has a diverse community of at least 7 primate species (Pollard *et al.*, 2007), 6 of which are classified as threatened by the IUCN. The few dietary studies of the Indochinese Leopard conducted in evergreen forests in Thailand showed that it preys mainly on relatively small species, such as primates, small ungulates, and small carnivores (Grassman, 1999, Rabinowitz, 1989, Steinmetz *et al.*, 2013). In contrast to Thailand, the EPL is dominated by dry open forest which supports a higher ungulate biomass (Gray *et al.*, 2012c) and presumably lower primate density. However, the extent to which Leopard use the potential prey species in this habitat type is unknown, although such information is important to provide insight into the predatory niche of Leopard in the community, and determine whether Leopard predation negatively impacts threatened prey populations.

Male Leopard is 30-50% larger in body mass than female (Skinner and Chimimba, 2005), similar to the sex differences found in other large felids, which may result in inter-sexual differences in diet and prey selection. For example, male Cheetah (*Acinonyx jubatus*) and male Cougar (*Puma concolor*) were shown to prey on larger ungulate species than females (Anderson and Lindzey, 2003,

Knopff *et al.*, 2010, Rostro-García *et al.*, 2015). However, such sex-specific differences have not yet been investigated for Leopard in Asia.

The purpose of this study was to investigate the ecology of the last potentially viable population of Indochinese Leopard in Cambodia, at a globally important priority site for the subspecies. The specific objectives were to: estimate the density of Leopard; determine the diet and prey selection of Leopard, with a focus on differences between males and females; and determine predation impact of Leopard on the community of threatened ungulate species in SWS, the largest protected area within the EPL. We predicted that: (i) the Leopard density would have decreased, owing to recent increases in poaching in the region; (ii) Leopard diet would be dominated by primates, small (<30 kg) ungulates, and other small prey; (iii) Leopard would selectively consume prey weighing 10-40 kg, given its preferred prey range (Hayward *et al.*, 2006); (iv) in general, male and female Leopard would consume similar-sized prey species; and (v) predation impact would be higher for small ungulate species. In order to meet the objectives, we used DNA confirmed Leopard scats, camera-trap and line-transect data from SWS.

5.3 Materials and methods

5.3.1 Study area

The SWS (3,725 km^2), formerly named Mondulkiri Protection Forest up to 2016, is located in eastern Cambodia within the EPL, a complex of protected areas covering >10,000 km^2 (Gray and Prum, 2012). A core zone (approx. 1,700 km^2) is located in the eastern part of SWS. There are 5 ranger stations located throughout SWS that are permanently manned by rangers, 3 of which are within or bordering the core zone, in addition to several substations that are manned by rangers periodically. No villages occur within SWS core zone, although several villages occur along the northern, western, and southern areas of SWS. Local villagers are allowed to enter SWS to collect non-timber forest products, graze cattle, fish, and hunt unprotected species for subsistence using traditional methods.

The habitat of SWS is dominated by open dry deciduous dipterocarp forests, interspersed with smaller patches of mixed deciduous, evergreen, semi-evergreen, and riverine forests. The SWS has a distinct dry season for approximately half the year (December to May), followed by a rainy

season (June to November). There are 7 species of ungulates in SWS (Gray *et al.*, 2012c), several of which are classified as Threatened (IUCN classification follows each name), including Banteng (EN), Eld's Deer (EN), Wild Water Buffalo (*Bubalus arnee* - EN), Sambar (*Rusa unicolor* - VU), Gaur (*Bos gaurus* - VU), Eurasian Wild Pig (*Sus scrofa* - LC; hereafter Wild Pig), and Red Muntjac (*Muntiacus vaginalis* - LC; hereafter Muntjac). There are at least 7 primate species in EPL (Pollard *et al.*, 2007), which include the Red-cheeked Gibbon (*Nomascus gabriellae* - EN), Stump-tailed Macaque (*Macaca arctoides* - VU), Pygmy Slow Loris (*Nycticebus pygmaeus* - VU), Black-shanked Douc (*Pygathrix nigripes* - EN), Long-tailed Macaque (*Macaca fascicularis* - LC), Northern Pig-tailed Macaque (*Macaca leonina* - VU), and Indochinese Langur (*Trachypithecus germaini* - EN), the latter 5 species having been confirmed in SWS. The Tiger was recently extirpated in EPL (O'Kelly *et al.*, 2012), and in SWS the last Tiger photograph and paw print were recorded in 2007 and 2009, respectively. Other felid species recorded in EPL that potentially occur in SWS include Asiatic Golden Cat (*Catopuma temminckii* - NT), Clouded Leopard (*Neofelis nebulosa* - VU), Jungle Cat (*Felis chaus* - LC), Leopard Cat (*Prionailurus bengalensis* - LC), and Marbled Cat (*Pardofelis marmorata* - NT). Other carnivore species include Golden Jackal (*Canis aureus* - LC), Dhole (*Cuon alpinus* - EN), and at least 10 species of smaller carnivores (Gray *et al.*, 2014b).

5.3.2 Camera trapping and density estimation

In order to compare our survey results to those obtained in 2009, we followed the same field methodologies reported by Gray and Prum (2012). Consequently, we used the same camera traps (Reconyx RapidFire Professional PC90; Reconyx, Inc., Holmen, WI, USA) during the same season (i.e., dry season) and placed them in pairs along the same roads and trails, with the same spacing (2-3 km) between camera stations (Gray and Prum, 2012). Cameras were placed on trees located 2-3 m from the middle of the trail, and motion beams set to trigger at a height of 40-45 cm above the centre of the trail. We extended the area surveyed by Gray and Prum (2012), from 210 km^2 to approximately 270 km^2, to include roads and trails to the north and northwest (Figure 5.1), in an attempt to record additional Leopard based on signs we observed. We used 42 paired camera stations that were set out in two blocks (each with 21 locations) due to the limited number of cameras (n = 42). We camera

trapped the northern block from 18 February to 9 April 2014, and the southern block from 9 April to 3 June 2014. Cameras were operational for 24 hours during the sampling sessions, and checked approximately halfway through each session within a block to change batteries and remove vegetation.

Two of the authors independently identified individual Leopard based on its unique pelage markings, and any discrepancies were jointly reviewed to reach a final agreement on identification. Because Leopard has low detection probabilities, individual capture histories were developed considering a 48-hour period as one occasion, such that 1 encounter occasion consisted of a 2-day sampling period, and a binary matrix of Leopard captures was constructed (i.e., detection history of individuals collated). The data were collapsed in this manner to avoid estimated detection rates close to 0 (photographic detections were sparse), as this can lead to estimation problems (Rich *et al.*, 2014).

The demographic parameters of wild Indochinese Leopard are unknown. As a consequence, it is difficult to estimate the time frame that adequately approximates a closed population. Relatively few test for population closure have been developed in traditional capture-recapture (Otis *et al.*, 1978, Stanley and Burnham, 1999), mostly because violation of demographic closure can be indistinguishable from behavioural variation in detection (Soisalo and Cavalcanti, 2006). In addition, closure tests are limited in obtaining reliable estimates when small sample sizes are used (Kawanishi and Sunquist, 2004). In general, studies that focus on elusive species, such as the Indochinese Leopard, have low sample sizes, and thus these tests might not be appropriate for revealing robust values (Weingarth *et al.*, 2015). Similarly, no specific population closure test for spatially explicit capture-recapture (SCR) models is available, given that violation of population closure cannot be distinguished from the violation of other model assumptions . In the absence of suitable closure tests, a survey-period of 2-3 months was suggested to be appropriate for the study of felids (Karanth and Nichols, 1998, Weingarth *et al.*, 2015), including Leopards (93 days; Hedges *et al.*, 2015). We used a 98-day subset of our data to estimate Leopard density because we deemed this a period that would provide sufficient data for a species that has low-capture probability, while ensuring demographic closure and minimising the likelihood of activity centres changing considerably.

In order to compare the results with those obtained by Gray and Prum (2012), density was estimated using SCR models and the maximum-likelihood estimator DENSITY (DENSITY 5.0). Following Gray and Prum (2012), we set a buffer width around the trapping grid of 10 km, assumed a half-normal spatial capture probability function and a Poisson distribution of home-range centres. In addition, Leopard density was estimated using a 20 and 30 km buffer around the trapping grid (Table A5.1).

Bayesian inferences, unlike likelihood based procedure, do not rely on asymptotic arguments and are valid irrespective of sample size (Royle *et al.*, 2009a). Therefore, given the relatively low number of both individuals and recaptures, we also estimated density using the Bayesian estimator SPACECAP (version 1.1.0; Gopalaswamy *et al.*, 2012) of R version 3.2.3 (R Core Team, 2015). This spatial estimator requires 3 input files: (i) a trap deployment file; (ii) a detection history or capture file; and (iii) potential home-range centre file (demarcating potential home-range centre of Leopard within suitable Leopard habitat). For Bayesian models, we generated a 15 and 30 km buffer around a grid of equally spaced points (580 m intervals), containing the trap array, to represent the probable Leopard activity centres (Royle *et al.*, 2009a, Royle *et al.*, 2009b). Because the Leopard is a habitat generalist and the core area was surrounded by forested areas, we considered the totality of the buffer area as suitable habitat, and therefore the activity centres were assumed to be uniformly distributed over this space. In addition, during the dry season there is no body of water that could impede the movement of Leopard within the landscape. We used 70,000 Markov Chain Monte Carlo (MCMC) iterations, with the initial 20,000 values discarded during the analysis (burn-in period), and the data augmentation value was set to 10-30 times the number of photographed individuals. Models were run considering a global behavioural response (trap response absent), and fitted using a half-normal detection function and Bernoulli encounter model. The fit of each model was evaluated using the Bayesian *p*-value (Gelman *et al.*, 1996), where extreme values (near 0 or 1) indicated a lack of model adequacy, whereas values near 0.50 indicated model adequacy. Model parameters were adjusted until convergence was adequate (Geweke z-scores between −1.6 and +1.6), Bayesian *p*-values indicated model adequacy, and data augmentation, state-space extent and sample size were sufficiently large.

5.3.3 DNA analyses of scats

During the dry seasons of 2013 and 2014, scats (i.e., faeces) were collected along 30 transects (2-km each) established on roads throughout the core zone of SWS, as well as opportunistically when conducting other research. For each scat, maximum diameter was measured (unless the scat was deteriorated) and GPS location was recorded. Approximately 10 g of each scat was stored in small paper envelopes, and then sent to the Sackler Institute for Comparative Genomics, American Museum of Natural History, for genetic analysis to determine species, individual, and sex. For species determination, genomic DNA was extracted and species were identified from scat as described in Caragiulo *et al.* (2014). Scat samples were identified to species by amplifying regions of 4 mitochondrial genes. PCR amplicons were sequenced as described in Caragiulo *et al.* (2014) using the thermocycler profile of Platt *et al.* (2007). We purified sequencing amplifications via ethanol precipitation and sequenced them in an ABI 3730xl DNA Analyser (Applied Biosystems, Carlsbad, CA, USA). We manually edited sequences using Geneious (www.geneious.com) version 8.0 (Kearse *et al.*, 2012), and compared them to both an in-house database of carnivore mtDNA sequences and the NCBI nucleotide BLAST database (Benson *et al.*, 2013) to confirm species identification.

All scat samples identified as Leopard were processed for individual and sex identification. Leopard samples were amplified using 12 microsatellite loci to identify individuals as described in Caragiulo *et al.* (2015). The sex of each sample was determined by amplifying portions of the zinc finger on the X and Y chromosomes (Wei *et al.*, 2008) using the protocol described in Caragiulo *et al.* (2015). Each amplification was independently repeated a minimum of 4 times for both individual and sex identification (see Caragiulo *et al*. 2015 for more details).

5.3.4 Diet and prey selection

The diet of Leopard was determined by the analysis of the confirmed Leopard scats, after washing them in a laboratory and drying the remains. For each scat, we separated hairs, claws, hoofs and bones from different prey species, and estimated percent volume of each species. Prey items that were 1% or less of scats were excluded from analysis. Hair samples were identified to species by

examining the structure of the medullas, which became visible under the microscope after soaking hairs in xylene for 24 hours. Medulla structures were compared to those in a reference collection of hairs from known species. Hairs of Leopard were found in some scats, although in trace amounts (≤5%), and these were excluded from analysis because we assumed they were ingested while grooming.

Results from scat analysis were quantified in terms of frequency of occurrence (i.e., percentage of scats containing a particular food item) for comparison purposes (Klare *et al.*, 2011). However, because the frequency of occurrence can be misleading given that smaller prey species contribute more to a scat than larger species (Karanth and Sunquist, 1995, Klare *et al.*, 2011), we obtained the percent biomass consumed (BC). The percent BC, considered the best approximation of the true diet (Klare *et al.*, 2011), was calculated using a regression equation derived from feeding trials on captive Cougar (Ackerman *et al.*, 1984). Cougar is similar to Leopard in body size and niche, thus we assumed they would have a similar prey spectrum and therefore the model would be applicable to Leopard (Klare *et al.*, 2011), and this method has been used by previous studies to estimate Leopard diet (Andheria *et al.*, 2007, Athreya *et al.*, 2014, Harihar *et al.*, 2011, Karanth and Sunquist, 1995, Kumaraguru *et al.*, 2011, Odden and Wegge, 2009). In the regression equation, $Y_i = 1.98 + 0.035X_i$, X is the live body mass of prey, whereas Y is the mass of prey per collected scat (i). The mean live body mass of all prey species was taken from Francis (Francis, 2008). For all species <30 kg, we used the adult weight, or the mean of adult males or females if both were given. If we could not distinguish hairs between two species (e.g., Black-shanked Douc and Indochinese Langur), then we took the mean of weights given for those two species. For ungulates >30 kg (i.e., Banteng and Wild Pig) we used half the weight given for adult females, assuming Leopard killed both adult females and young. We excluded arthropods and unknown mammal (total 3 scats) from the biomass calculations because we were unable to accurately estimate BC for these prey items.

We calculated Jacobs' index D (Jacobs, 1974): $D = (r - p) / (r + p - 2rp)$, where r is the fraction of prey used, and p is the fraction of prey available. Jacobs' indices were calculated to investigate prey selection using biomass data to assess which prey species were selected ($0 < D \leq 1$) and which were avoided ($-1 \leq D < 0$). For each prey species, the D-value depends on which other

species are included in the calculation, therefore, we calculated *D*-values only for the 3 ungulate species that were consumed by Leopard. To determine fraction of prey available, we used ungulate densities estimated by WWF Cambodia personnel. Ungulate densities were estimated using distance-based line transect sampling (Buckland *et al.*, 2001), following the same field protocols and transects of Gray *et al.* (2012c). During the dry season of 2014, a total of 38 transects (2-3 km in length) were surveyed 4-8 times within the SWS core zone (approx. 1,700 km^2). A total of 603 km was walked across all transects, with observers walking transects just after sunrise (start time = 05:00-07:30) and just prior to sunset (start time = 15:30-17:30). Data recorded for ungulates included: species; number of animals (cluster size); distance between the animal or centre of animal group and the observers (using laser rangefinders); compass bearing to the animal or animal group, and; compass bearing of the transect line. Data were analysed using the program DISTANCE v.6.2 (Thomas *et al.*, 2010). In order to fit detection functions, number of encounters per species were pooled across two adjacent protected areas, SWS and Phnom Prich Wildlife Sanctuary (PPWS), and densities were calculated only for those ungulates that had the minimum of 40 observations (Buckland *et al.*, 2001; see Gray *et al.*, 2012b for more details). Species data were pooled from 2010, 2011 and 2014 to produce a global detection function. Densities were then stratified by protected area and year to obtain ungulate densities for SWS. Biomass available for each ungulate species was obtained by multiplying the density estimates by the adult female weights given by Francis (2008).

We calculated Leopard diet and *D*-values based on all confirmed Leopard scats that were collected, and then calculated diets and *D*-values for males and females separately based on the subset of scats that were assigned to sex. For scats assigned to different individuals, we calculated and compared the diet of individuals with ≥5 scats for illustrative purposes only.

We calculated predation impact on ungulates from an equation used previously for carnivores (Jedrzejewska and Jedrzejewski, 1998, Klare *et al.*, 2010): $N_{prey} = (D \times DFI \times B_{prey} \times n_{days} \times 100) / BM_{prey}$, where N_{prey} is number of prey individuals consumed by Leopard/100 km^2, D is density of Leopard/km^2, DFI the daily food intake of Leopard, B_{prey} is the percent biomass consumed by Leopard for a given prey species, n_{days} the number of days (i.e., 180 days representing the dry season), and BM_{prey} the mean live body mass of prey. The DFI for Leopard was assumed to be 4.01

kg, based on the average of four different studies that calculated DFI for Leopard (Bailey, 1993, Bothma and le Riche, 1986, Odden and Wegge, 2009, Stander *et al.*, 1997). The BM_{prey} was taken from Francis (2008). For each ungulate species, N_{prey} was divided by density (individual/100 km^2) to determine the percent of ungulate population consumed by Leopard. Predation impact could only be calculated for the 6-month dry season, as this was the only season we collected scats. Scats collected from two consecutive dry seasons were pooled in analysis.

5.4 Results

From 2,147 trap days, we obtained a total of 26 independent events from 8 confirmed different Leopards: 6 were photographed on both flanks, 2 were photographed only on their right flank and 1 was photographed only on its left flank, thus the total number of Leopard was 8 or 9. For analyses, we assumed 8 different Leopards were photographed (2 females, 2 males, and 4 of unknown sex). Given that some individuals were captured more than once by the same camera trap within a 48-hour period, a total of 23 capture events were used in subsequent analyses. Using maximum-likelihood inference, the estimated density (± SE) was 1.0 ± 0.4 Leopard/100 km^2, which was 72% lower than the density of 3.6 ± 1.0 Leopard/100 km^2 estimated from 2009 using the same analysis (Gray and Prum, 2012). The density estimate was the same regardless of whether we used a 10, 20 or 30 km buffer (Table A5.1). Using Bayesian inference, the estimate (posterior mean) of Leopard density was of 1.0 Leopard/100 km^2 (Post. SD = 0.4; Table A5.2).

Six ungulate species were recorded during the line-transect surveys in SWS and PPWS, which included Muntjac (*n* = 115), Wild Pig (*n* = 58), Banteng (*n* = 44), Gaur (*n* = 5), Eld's Deer (*n* = 5), and Sambar (*n* = 1). Mean (± SE) densities were 2.1 ± 0.3 Muntjac/km^2, 6.5 ± 2.0 Wild Pig/km^2, and 2.2 ± 0.5 Banteng/km^2.

A total of 113 putative Leopard scats was collected, and 73 were confirmed by genetic analysis to be Leopard. Of the 40 scats not confirmed to be from Leopard, 23 failed to detect any species, 9 were identified as Dhole, 3 were identified as Golden Jackal or Dog (*Canis lupus familiaris*), 3 were identified as prey, and 2 detected multiple carnivore species. Individual assignment was possible for 44 of the 73 confirmed Leopard scats. When considering only scats that

were collected from within the camera trapping grid during our survey period in 2014, 9 different Leopards were identified (4 males, 3 females, 2 unknown), 7 of which had >1 scat collected. The 9 different Leopards identified from scats correspond to the maximum number of individuals identified from the camera-trap photos.

Sex could be assigned to 43 (23 males, 20 females) of the 73 confirmed Leopard scats. Mean diameter (± SD) of confirmed Leopard scats was 3.1 ± 0.4 cm (range: 2.1-4.0; n = 53), with a mean diameter of confirmed male scats of 3.2 ± 0.4 cm (range: 2.6-4.0 cm; n = 15) and of confirmed female scats of 2.9 ± 0.3 cm (range: 2.4-3.3 cm; n = 15).

The 73 Leopard scats contained a total of 103 items, comprising 13 prey species, ranging in size from insect to Banteng (Table 5.1). A total of 63.0% of scats contained 1 prey item, whereas 32.9% of scats contained 2 prey items, and 4.1% of scats contained 3 prey items. Ungulates comprised 86.5% of biomass consumed (BC), followed by Malayan Porcupine (*Hystrix brachyura* hereafter porcupine, 4.3% BC), small carnivores (3.7% BC), and primates (3.5% BC, Table 5.1). Banteng was the most consumed ungulate (42.2% BC), followed by Muntjac (22.1 % BC), and Wild Pig (22.1% BC; Table 5.1). The biomass of ungulates consumed during the dry season did not reflect the biomass available, as Leopard showed a strong positive selection for Muntjac (D = 0.87), non-selection for Wild Pig (D = -0.02), and negative selection for Banteng (D = -0.45; Figure 5.2). Leopard consumed 6.7 individual Muntjac/100 km^2 (3.2% of the Muntjac population), 4.3 individual Wild Pig/100 km^2 (0.7%), and 1.0 individual Banteng/100 km^2 (0.5%) during the dry season.

When diets were analysed separately by sex, the results showed that male and female Leopard had similar diets across 5 broad prey categories (Table 5.1; Figure 5.3). Male and female diets were comprised mainly of ungulates (84.7 and 87.4% BC, respectively), whereas consumption of the other prey categories was <7% each (Table 5.1; Figure 5.3). However, when ungulate species were analysed separately, male, and female Leopard had opposite trends in consumption with regard to ungulate body size (Figure 5.4). Male Leopard consumed mainly Banteng (61.5% BC) which was nearly 10 times the amount of Muntjac consumed (6.5% BC; Figure 5.4). In contrast, female Leopard consumed mainly Muntjac (55.7% BC) and had only a trace amount of Banteng in its diet (<1% BC; Figure 5.4). Male and female Leopard consumed Wild Pig in moderate amounts (16.6% and 31.3%,

respectively; Figure 5.4). When compared with availability, consumption of all 3 ungulate species by male Leopard was approximately in proportion to their biomass available (Figure 5.4). By contrast, female Leopard exhibited a strong positive selection for Muntjac (D = 0.97) and a strong negative selection for Banteng (D = -0.99; Figure 5.4).

The diets of 3 male Leopard hinted at individual specialisations. One male (n = 7 scats) consumed mostly Banteng (71.5% BC), a second male (n = 6 scats) consumed less Banteng (40.1%) and more small (<10 kg) species, whereas a third male (n = 5 scats) did not consume Banteng, and instead consumed mostly Wild Pig (50.0%) and porcupine (34.3%).

5.5 Discussion

The density of 1.0 Leopard/100 km^2 in SWS was one of the lowest densities reported in Asia. Previous studies using SCR models in Malaysia, Bhutan, Nepal, and India showed Leopard densities typically were 3-5 Leopard/100 km^2 (Borah *et al.*, 2014, Hedges *et al.*, 2015, Selvan *et al.*, 2014, Thapa *et al.*, 2014), even in unprotected, human-dominated landscapes (Athreya *et al.*, 2013), and up to 9-13 Leopard/100 km^2 (Carter *et al.*, 2015, Goldberg *et al.*, 2015, Kalle *et al.*, 2011). Only a population of the Critically Endangered Amur Leopard was found to have similarly low densities of 1 Leopard/100 km^2 (Vitkalova and Shevtsova, 2016). In our study, both methods for estimating density showed nearly identical results, and the camera-trap data showed a similar minimum number of individuals within the camera-trapping grid as the DNA analysis of scats (8 or 9 Leopards and 9 Leopards, respectively), suggesting our density estimate for the core zone of SWS was reliable.

The 72% decrease of Leopard density in the core zone of SWS from 2009 to 2014 was not likely due to methodologies, because we used the same analysis and followed the same field protocols as the study in 2009 (Gray and Prum, 2012). Similarly, the density decline of Leopard was not likely due to prey declines, because densities of Banteng, Wild Pig, and Muntjac remained stable or increased in SWS from 2009-2011 to 2014 (Gray *et al.*, 2012c). Although we predicted that the Leopard density would decline due to regional Leopard declines and recent increases in poaching, we did not expect such a large decline. This is one of the largest density decreases recorded in a Leopard population, and suggests the Leopard population in SWS is rapidly heading towards

extinction. Only two previous studies found a >60% decrease in a Leopard density in <6 years, which was attributed to an increasing density of reintroduced Tiger inside protected areas in India (Harihar *et al.*, 2011, Mondal *et al.*, 2012a).

Reasons for the rapid decline of Leopard in SWS since 2009 are likely due to increases in poaching, particularly indiscriminate snaring. Across Southeast Asia, deforestation rates have increased recently to become the highest in the world, which has coincided with an explosion in the illegal wildlife trade fuelled by increased demand, thereby causing serious declines in many wildlife species (Duckworth *et al.*, 2012, Gray *et al.*, 2017, Lynam, 2010), including Leopard (Rostro-García *et al.*, 2016a). Demand is often highest for those species used in traditional Asian medicine such as Tigers, and consequently these species have seen drastic declines and extirpations throughout the region (Lynam, 2010, Walston *et al.*, 2010). Although Tiger parts are worth more than Leopard parts, the latter are used as substitutes for Tiger parts in traditional Asian medicine given their higher availability (Raza *et al.*, 2012) or accessibility, thereby causing increased demand and higher prices for Leopard parts, especially when Tiger numbers decrease. The factors affecting Leopard and other wildlife declines in EPL are a microcosm of Southeast Asia, as recent increases in illegal logging in EPL coincided with an explosion in the illegal wildlife trade. Consequently, Tiger recently became extirpated in EPL (O'Kelly *et al.*, 2012) and Leopard may be following the same fate. In particular, indiscriminate snaring for the illegal bushmeat market may be the greatest factor causing the rapid decline of Leopard in SWS, as blanket snaring for common species such as Wild Pig and Muntjac has been increasing in the area even within protected areas (Gray *et al.*, 2017). The increase in snaring has led to the recent documentation of a Leopard killed by poachers in SWS (Gray, 2013) suggesting that high rates of poaching of Leopard are probably happening throughout SWS, and likely throughout EPL. Establishment of new roads, and improvements to existing roads, during the past 7 years have dramatically increased accessibility to all the protected areas and their core zones in EPL. The SWS is the largest and arguably best protected area in EPL with the lowest level of human disturbance. Additionally, the core zone in SWS contains several ranger stations and is located in the most remote part of the reserve. That Leopard density declined so dramatically in the core zone of SWS suggests that Leopard numbers elsewhere in EPL might have declined as rapidly, or even more

rapidly. In order to save this critical population of Leopard, not only do effective law enforcement activities need to increase in SWS and the other protected areas of EPL, but education campaigns are required to decrease the demand for bushmeat, as this leads to indiscriminate snaring across vast areas. In SWS, snaring appeared to have caused a dramatic decline in the Leopard population, while the ungulate populations remained stable. This was likely due to the presumably larger home ranges and lower population growth rates of Leopard compared to Muntjac, Wild Pig, and Banteng, thereby causing the Leopard population to be more negatively impacted by mortalities from snaring than the ungulate populations.

Contrary to previous studies in Thailand that showed the diet of Indochinese Leopard was dominated by relatively small prey, including primates, small ungulates, and small carnivores (Grassman, 1999, Rabinowitz, 1989, Steinmetz *et al.*, 2013), the Leopard diet in SWS was dominated by large (>30 kg) ungulates (64.3% BC), which did not support our prediction. In Africa, Leopard also feed mainly on large ungulates in open habitats (Bailey, 1993, Balme *et al.*, 2017a, Hirst, 1969, Mann, 2014, Mills, 1984, Pienaar, 1969, Stein *et al.*, 2015). Leopard may have had similar dietary niche in EPL as the African sites because open habitats typically have a higher carrying capacity for large ungulates than closed forests, resulting in Leopard predating more on large ungulates in open habitats due to their higher availability and/or accessibility.

The diameter of confirmed Leopard scats in SWS had a considerably wider range (2.1-4.0 cm) than previously reported for Leopard in Thailand (2.0-3.0 cm, Rabinowitz, 1989) and Africa (2.0-3.0 cm, Stuart and Stuart, 1994; 1.9-3.2, Bodendorfer *et al.*, 2006). Thus, some Leopard scats, particularly those of males, are larger than previously reported. In addition, diameter of Leopard scats in our study overlapped the confirmed scat diameters of both larger and smaller sympatric carnivores in Asia, such as Tiger, Dhole, and Asiatic golden cat (Kawanishi and Sunquist, 2008, Vongkhamheng, 2011). Therefore, we suggest that genetic analysis should be used in all future studies in Asia that investigate diets of Leopard and other sympatric carnivores based on scat analysis.

Our results are the first to record Leopard consumption of Banteng, which was also the main prey of Leopard in SWS (42.2% BC), especially for male Leopard (61.5% BC). Adult Banteng weigh

600-800 kg (Francis, 2008), and consequently the Leopard in SWS are the only known Leopard population in the world whose main prey had adult weight >500 kg. Prey species with adult weight >500 kg have been found before in Leopard diets in Africa and Asia, but they typically comprise trace amounts of <2% of the diet (Hayward *et al.*, 2006). Wild Pig (75-200 kg) also was regularly consumed by Leopard in SWS, comprising 22.1% BC, indicating Leopard consistently predated on ungulates with some the largest adult weights in SWS. Most previous studies showed that Wild Pig was avoided by Leopard, and consequently Wild Pig typically comprised only minor parts of Leopard diet, presumably because Wild Pig is relatively large and dangerous prey for Leopard (Hayward *et al.*, 2006, Karanth and Sunquist, 1995, Ramakrishnan *et al.*, 1999). Only Leopard in Golestan National Park (GNP), Iran, was shown to consume higher amounts of Wild Pig than in our study (Ghoddousi *et al.*, 2017). Ghoddousi *et al.* (2017) concluded high consumption of Wild Pig by Leopard in GNP was not due to a preference for Wild Pig, but rather due to the high numbers of that prey species on their study site, and the same was likely true in our study (see below).

In addition to ungulates, the next most consumed prey were porcupines, primates, and small carnivores (approx. 4% BC each; Table 5.1). Porcupines are relatively dangerous prey for large felids, as both Leopard and Cougar reportedly have died from injuries from porcupines (Elbroch *et al.*, 2016, Swanepoel *et al.*, 2014). That 9.6% of Leopard scats in SWS contained porcupine quills indicates this species was regularly consumed by Leopard. The regular consumption of porcupine could have been due to food stress, as porcupine predation by Cougar was shown to increase when primary prey decreased (Sweitzer *et al.*, 1997). Alternatively, subadults can prey on porcupines more than adults among large felids (Elbroch *et al.*, 2017), indicating it could have been younger Leopard that preyed upon porcupine in SWS. Consumption of primates and small carnivores by Leopard in SWS was lower than that reported in Leopard diets in Thailand (Grassman, 1999, Rabinowitz, 1989, Steinmetz *et al.*, 2013). The relatively low consumption of primates and small carnivores in SWS may have been due to lower availability compared to Thailand. Alternatively, high consumption of large ungulates by Leopard in SWS probably decreased their dependence on smaller prey species compared to Thailand.

Prey selection of Leopard in SWS was typical of that found in previous studies, as Leopard selectively consumed Muntjac, the smallest ungulate species (20-28 kg), which supported our prediction. Leopard consumed Wild Pig in proportion to availability, and consumed Banteng less than expected compared to availability. Thus, our results support previous research that showed preferred prey of Leopard is 10-40 kg (Hayward *et al.*, 2006). Our results indicate the relatively high consumption of Banteng and Wild Pig by Leopard in SWS was due to the relatively high density and biomass of these two ungulate species, rather than a preference of these prey species by Leopard.

Male and female Leopard had remarkably similar diets across prey categories, which supported our prediction. However, male, and female Leopard had opposite trends with regard to ungulate body size and consumption. Although sample sizes of male and female scats may not have been large enough to determine the full spectrum of their respective diets, we consider it was adequate to demonstrate major differences in consumption patterns between the sexes. In general, male Leopard consumed ungulates in proportion to availability, and consequently Banteng dominated its diet (Figure 5.4). By contrast, female Leopard had a strong positive selection for Muntjac, which dominated its diet, and had only a trace amount of Banteng. Our results regarding large differences in male and female diets were unexpected, given that previous studies in Africa did not find major differences in body size of ungulates consumed by male and female Leopard (Bailey, 1993, Stander *et al.*, 1997). In one exception, Balme *et al.* (2017a) found male Leopard consumed prey that was on average 1/3 larger than prey consumed by females. By contrast, our results showed that the main prey consumed by male Leopard in SWS was probably 12-30 times larger (depending on age of prey) than the main prey consumed by females. For Cougar and Cheetah, males were sometimes found to kill larger prey species than did females (Anderson and Lindzey, 2003, Knopff *et al.*, 2010, Rostro-García *et al.*, 2015), although the difference in prey size was not as great as in our study.

There may have been several reasons for the high consumption of Banteng by male Leopard in SWS. Firstly, male Leopard appeared to be non-selective in their consumption of all the ungulate species, thus the high consumption of Banteng was likely related to the high availability of this species in SWS. Secondly, Tiger was recently extirpated from EPL (O'Kelly *et al.*, 2012), and

Banteng presumably was one of the main prey of Tiger in EPL (Gray *et al.*, 2012c). Therefore, after extirpation of Tiger, male Leopard may have expanded its dietary niche to include Banteng, whose biomass dominated the ungulate community (71.4% of all ungulate biomass available). In SWS, Banteng represent an abundant food resource for male Leopard, which previously would have been less accessible to it due to competition with the behaviourally dominant Tiger. Tiger can kill and displace Leopard, and consequently Leopard avoid Tiger by using suboptimal habitat where there is lower risk of encountering Tiger (Carter *et al.*, 2015, McDougal, 1988, Odden *et al.*, 2010, Rayan and Linkie, 2016, Seidensticker, 1976, Steinmetz *et al.*, 2013). Leopard also was shown consistently to prefer smaller prey species than did Tiger at sites where these species were sympatric, probably as a mechanism to reduce encounters with Tiger while hunting (Andheria *et al.*, 2007, Karanth and Sunquist, 1995, Kumaraguru *et al.*, 2011). In the absence of Tiger, however, Leopard consumed larger prey (Harihar *et al.*, 2011, Mondal *et al.*, 2012a), indicating prey size of Leopard is affected by Tiger presence. In Africa, Leopard regularly killed larger ungulate species, including adult Common Eland (*Tragelaphus oryx*) and Greater Kudu (*Tragelaphus strepsiceros),* in the absence of larger carnivores (Mann, 2014, Stein and Hayssen, 2013), demonstrating the ability of Leopard to expand its dietary niche in the absence of larger competitors. Similarly, Cougar was found to expand its dietary niche and prey on larger ungulates in the absence of competing large carnivores (Elbroch *et al.*, 2015). Female Leopard avoidance of Banteng in SWS and preference for smaller and less dangerous species such as Muntjac was likely related to its smaller body size compared to males. Interestingly, extirpation of Tiger in SWS may have inadvertently allowed Leopard sexes to occupy different dietary niches, possibly reducing intersexual competition for food resources.

Dhole also occurred in SWS, although its population was low during our study likely due to a disease outbreak (Kamler *et al.*, 2015). Even though Leopard and Dhole potentially competed for food resources, we assumed the Dhole population was unlikely to significantly affect the Leopard diet and prey selection due to the low numbers of Dhole on our study site. Nonetheless, further research is needed to better understand what effects, if any, Dhole have on Leopard ecology.

Accessible prey, defined as prey consumed both preferentially and in proportion to abundance, for African Leopards was recently determined to be 1-45 kg (Clements *et al.*, 2014b).

Our results suggest that male and female Leopard can have vastly different accessible prey size ranges, at least under certain conditions. In SWS, male Leopard consumed all ungulate species approximately in proportion to their availability, regardless of ungulate size and threat of injury. This indicates the accessible prey range of male Leopard in SWS ranged up to 600-800 kg for adult Banteng, or up to 300 kg for young Banteng, which is 7-13 times larger than that predicted by Clements *et al.* (2014b). By contrast, female Leopard selectively consumed Muntjac the most and Wild Pig secondarily, both of which were within the accessible prey range reported by Clements *et al.* (2014b), if we assume females were consuming mostly young Wild Pig. Additional research is needed to investigate further if male and female Leopard have different accessible prey ranges in other areas, as this has important implications regarding their prey requirements and predator-prey relationships.

Although samples from individuals were small, they suggested that 3 male Leopard have different specialisations, as Banteng ranged from 0 to 72% of their diets, indicating not all males preyed on Banteng to the same degree. Although sample size was small for the 3 individual males, we consider that our results show the potential for males to have different dietary specialisations within the same area, similar to that previously reported for large felids. For example, individual specialisation on prey species was shown to occur for African Leopard (Bailey, 1993, Mann, 2014) and Cougar (Elbroch and Wittmer, 2013, Kamler *et al.*, 2002, Lowrey *et al.*, 2016). Additionally, subadults prey on different species from adults among Leopard and Cougar (Anderson and Lindzey, 2003, Bailey, 1993, Elbroch *et al.*, 2017, Knopff *et al.*, 2010), leading to individual differences in diet and prey selection that change with age and social status.

Predation impact of Leopard in SWS was higher for Muntjac than Banteng and Wild Pig, which supported our prediction. That said, predation impact was low for all 3 ungulate species (<4% of populations), which was due to the relatively low Leopard density. Regarding threatened ungulate species, Leopard consumed only 0.5% of the Banteng population, and we did not detect any other threatened ungulates in the Leopard diet, suggesting Leopard did not negatively impact any threatened ungulate species during the study period. Regarding threatened primates, Leopard consumed Colobinae and *Macaca* spp., although in low amounts (1.9% and 1.6% BC, respectively).

Although we were unable to distinguish hairs among the macaque species, Long-tailed Macaque was very common in SWS, and we suspect most consumption of macaque was this species, rather than the threatened macaque species that were rare and possibly absent in the study site. Although we did not determine primate densities, Leopard predation likely did not negatively impact any primate populations, primarily because Leopard density was relatively low in SWS.

5.6 Conclusion

One of the last remaining potentially viable populations of the Indochinese Leopard in Southeast Asia, and the last population in Cambodia, occurs in EPL, and our results show this population is still functioning as part of an important large predator-prey ecosystem. Female Leopard fill a typical Leopard niche as predator of relatively small-sized ungulates, whereas male Leopard appeared to have expanded its dietary niche to include regular predation on Banteng, one the largest ungulate species. Consequently, male Leopard is filling the predatory niche of the largest carnivore, left open after the extirpation of Tiger. However, widespread poaching, which led to the extirpation of the Tiger in EPL, now has likely led to a 72% decline of the Leopard density in SWS over a 5-year period. Thus, immediate action is needed to prevent the loss of this unique Leopard population. Short-term solutions should include increasing the effective enforcement in SWS, such as increasing the number of rangers and anti-poaching units, coinciding with increases in patrols, sweeping areas to remove snares, and increasing check points and road blocks to prevent poachers from entering the core zone. Long-term solutions include education campaigns to reduce demand for bushmeat and wildlife parts at the provincial, national, and regional levels, as growing demand has led to recent increases in blanket snaring across vast areas (Gray *et al.*, 2017), including SWS. As a result of improved accessibility to and within the protected areas of EPL, transportation of wildlife products to urban hubs and across international borders is a relatively easy task. Therefore, the strength of transboundary collaborations among relevant bodies needs to be improved to reduce illegal wildlife trade. Other long-term solutions include starting eco-tourism in the area, to generate alternative income for local people, and education programmes highlighting the importance and benefits of

protecting the local wildlife. Only with the implementation of these short- and long-term actions will there be any hope for saving the last Leopard in Cambodia.

5.7 Acknowledgements

At the time, research in SWS was supported by the Forestry Administration of the Ministry of Agriculture Forestry and Fisheries. We thank K. Omaliss and A. Bousa for advice. We also thank T. N. E. Gray, L. Bora, and other WWF Cambodia staff for advice and support, as well as WWF research rangers in SWS for their assistance during the project. We thank Phnom Tamao Wildlife Rescue Center for providing hair samples, and Pannasastra University of Cambodia, Phnom Penh, for lending laboratory equipment. A Kirk Turner Scholarship supported SR-G while analysing and writing up. Funding for field work was provided by grants from the Mohamed bin Zayed Species Conservation Fund, People's Trust for Endangered Species, Taronga Foundation, and the Iris Darnton Foundation. WWF Cambodia provided the camera traps, field equipment, logistical support, and funding for field work using WWF US and Humanscale grants.

Table 5.1 Diet of the Indochinese Leopard (*Panthera pardus delacouri*), expressed as percentage of biomass consumed (% BC) and frequency of occurrence per scat (% FOS), in Srepok Wildlife Sanctuary, Cambodia. All scats included were confirmed by genetic analysis to be from Leopard, whereas male and female scats were a subset that were assigned to sex by genetic analysis.

Prey category	**All scats (*n* = 73)**		**Male (*n* = 23)**		**Female (*n* = 20)**	
Species	**% BC**	**% FOS**	**% BC**	**% FOS**	**% BC**	**% FOS**
Ungulate	**86.5**	**79.5**	**84.7**	**73.9**	**87.4**	**95.0**
Banteng (*Bos javanicus*)	42.2	17.8	61.5	30.4	0.5	5.0
Wild Pig (*Sus scrofa*)	22.1	39.7	16.6	43.5	31.3	30.0
Muntjac (*Muntiacus vaginalis*)	22.1	38.4	6.5	17.4	55.7	70.0
Carnivore	**3.7**	**9.6**	**2.5**	**8.7**	**3.7**	**5.0**
Small Indian Civet (*Viverricula indica*)	0.7	1.4	0	0	0	0
Common Palm Civet (*Paradoxurus hermaphroditus*)	2.2	6.9	2.5	8.7	0	0
Leopard Cat (*Prionailurus bengalensis*)	0.7	1.4	0	0	3.7	5.0
Primate	**3.5**	**8.2**	**4.9**	**13.0**	**3.9**	**10.0**
Macaque (*Macaca* spp.)	1.6	4.1	3.0	8.7	2.1	5.0
Colobinae (*Pygathrix nigripes* and/or *Trachypithecus germaini*)	1.9	4.1	1.9	4.4	1.8	5.0
Others						
Malayan Porcupine (*Hystrix brachyura*)	4.3	9.6	6.2	17.4	1.6	5.0
Burmese Hare (*Lepus peguensis*)	1.4	4.1	1.7	4.4	3.4	10.0
Small (<1 kg) Rodent	0.8	2.7	0	0	0	0
Unknown Mammal	---	1.4	0	0	0	0
Fresh-water Crab (Potamidae)	---	1.4	0	0	0	0
Termite	---	1.4	0	0	0	0

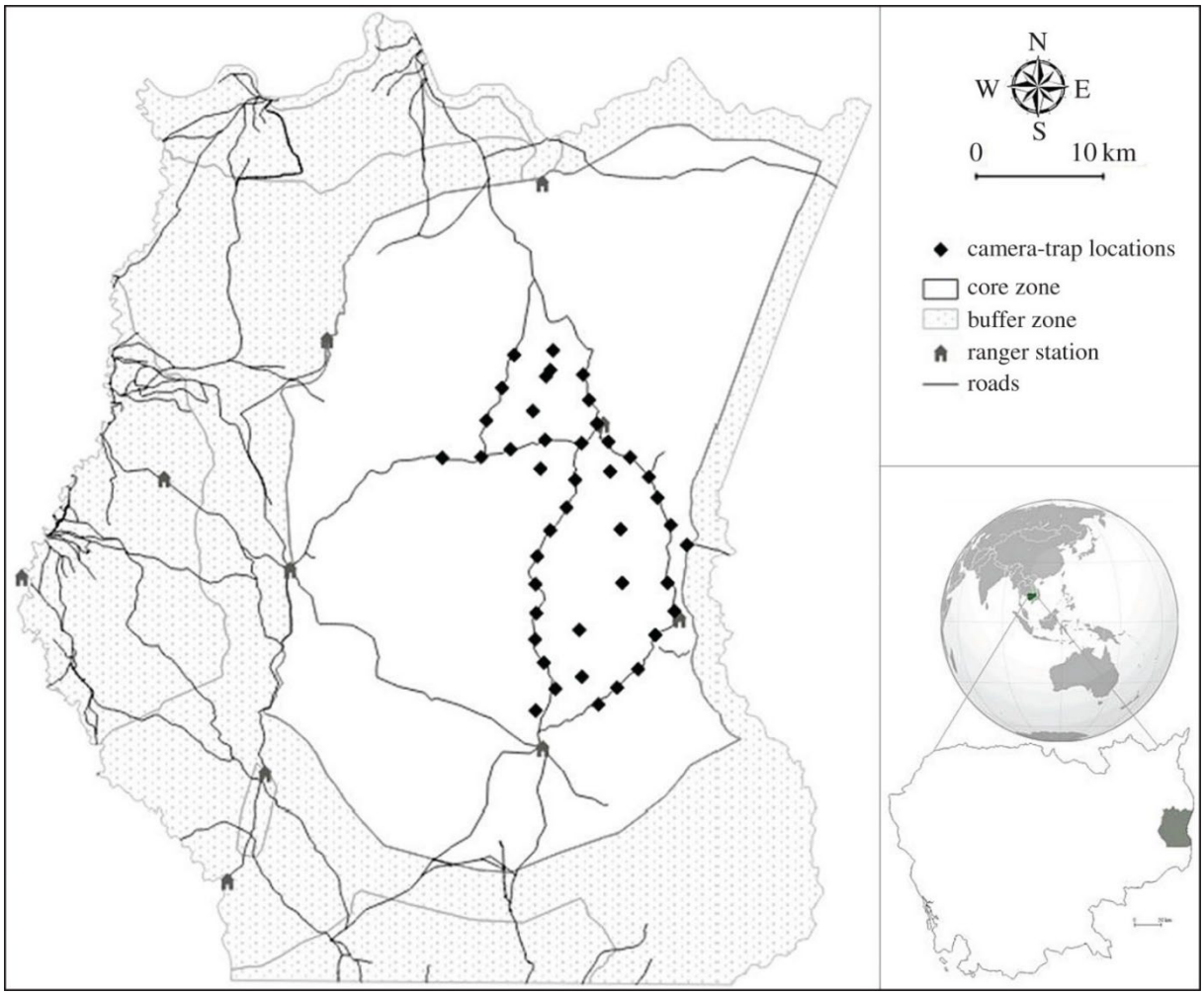


Figure 5.1 Map of Srepok Wildlife Sanctuary, Cambodia, indicating the camera-trap locations (*n* = 42) used to estimate the Indochinese Leopard (*Panthera pardus delacouri*) density in 2014. The inset on the right shows the location of Srepok Wildlife Sanctuary in Cambodia.

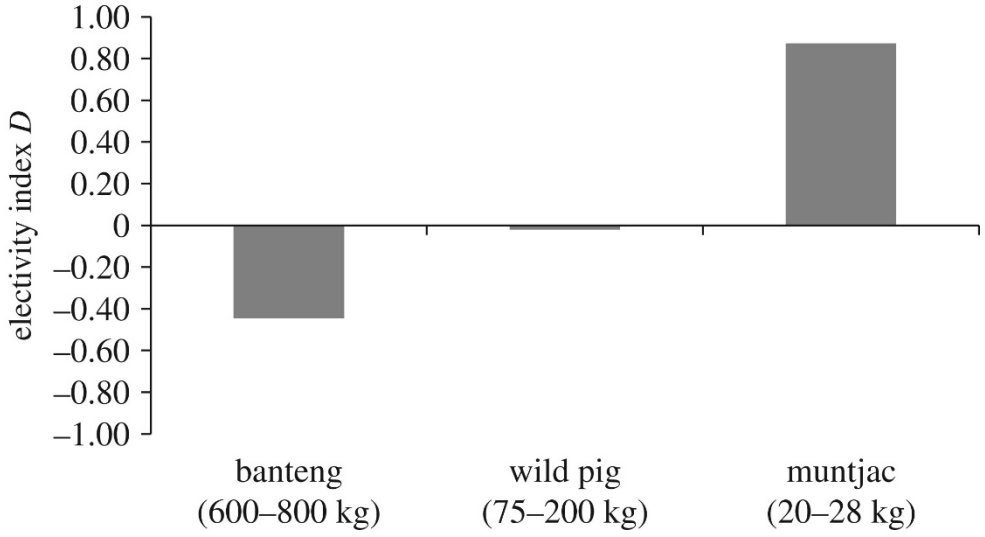


Figure 5.2 Jacob's electivity index (*D*) of the biomass of ungulates consumed by the Indochinese Leopard (*Panthera pardus delacouri*) in Srepok Wildlife Sanctuary, Cambodia.

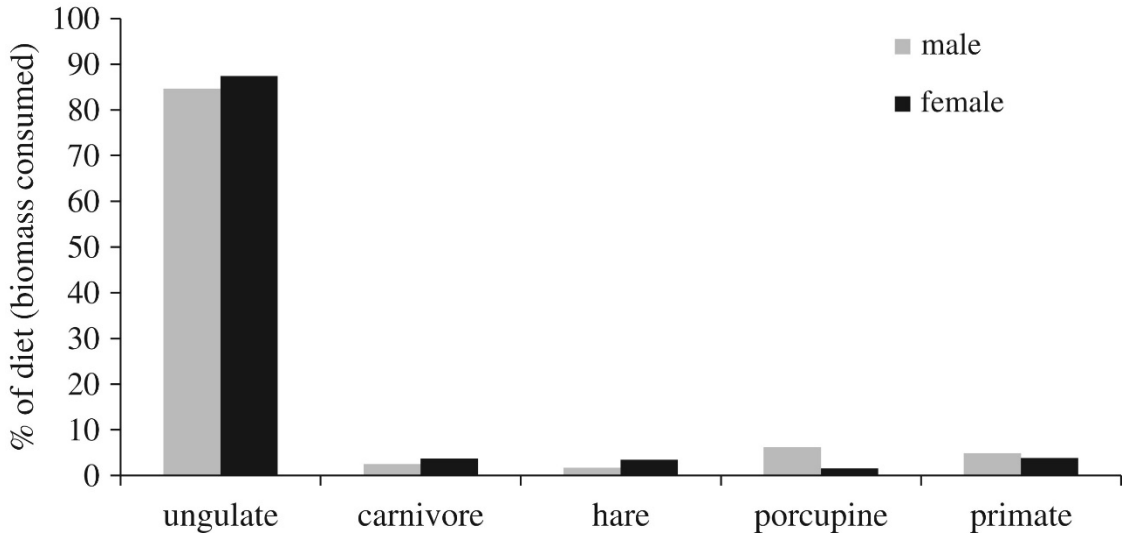


Figure 5.3 Diet of male and female Indochinese Leopard (*Panthera pardus delacouri*) based on biomass consumed of 5 main prey categories in Srepok Wildlife Sanctuary, Cambodia.

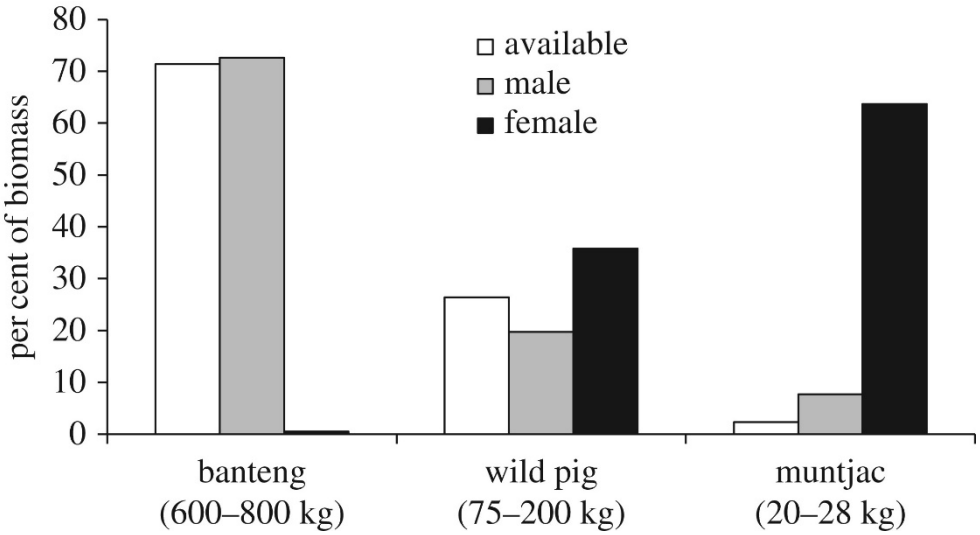


Figure 5.4 Biomass of ungulates consumed by male and female Indochinese Leopard (*Panthera pardus delacouri*) compared to biomass available in Srepok Wildlife Sanctuary, Cambodia.

5.8 Supplementary Material

Appendix 5.1 The mtDNA sequences were deposited in the Barcode of Life Database with accession numbers CBPPA001-17 through CBPPA015-17 (www.boldsystems.org).

Appendix 5.2 Supplementary tables

Appendix 5.2 Supplementary tables

Table A5.1 Summary statistics from spatially explicit capture-recapture models fitted to camera-trapping data on Indochinese Leopard (*Panthera pardus delacouri*) from Srepok Wildlife Sanctuary, Cambodia. D = density of Leopard per 100 km^2, g_0 = baseline trap encounter rate, σ = movement parameter (m), 95% CI = 95% Confidence Interval.

Buffer width	Parameter	Value	SE	95% CI
10 km	D	0.96	0.39	0.44-2.07
	g_0	0.01	0.01	0.01-0.03
	σ	3886.15	660.92	2791.17-5410.69
20 km	D	0.95	0.40	0.43-2.08
	g_0	0.01	0.01	0.01-0.03
	σ	3850.98	643.31	2781.98-5330.76
30 km	D	0.95	0.40	0.43-2.08
	g_0	0.01	0.01	0.01-0.03
	σ	3850.29	643.07	2781.66-5329.45

Table A5.2 Posterior summaries from spatially explicit capture-recapture models fitted to camera-trapping data on Indochinese Leopard (*Panthera pardus delacouri*) from Srepok Wildlife Sanctuary, Cambodia. D = density of Leopard per 100 km^2, λ_0 = baseline trap encounter rate, ψ = probability that an animal in the augmented data set is a real animal in the space state, N = number of individuals in the state-space, σ = movement parameter (m), 95% BCI = 95% Bayesian Credible Interval.

Buffer width	Parameters	Posterior mean	Posterior SD	95% BCI
15 km	D	0.99	0.35	0.42-1.64
	λ_0	0.03	0.01	0.01-0.05
	ψ	0.25	0.09	0.09-0.43
	N	21.10	7.40	9.00-35.00
	σ	4320.00	849.00	2870.00-6030.00
30 km	D	1.01	0.38	0.37-1.77
	λ_0	0.03	0.01	0.01-0.05
	ψ	0.29	0.11	0.11-0.53
	N	54.40	20.30	20.00-95.00
	σ	4280.00	842.00	2930.00-5940.00

CHAPTER 6

Fading spots: Population dynamics of the last Leopard population of eastern Indochina

6.1 Abstract

The Eastern Plains Landscape (EPL) of Cambodia has been identified as 1of 3 priority sites for the conservation of the Critically Endangered Indochinese Leopard (*Panthera pardus delacouri*) because it harbours the last viable population of Leopard in eastern Indochina. A decade ago, Srepok Wildlife Sanctuary (hereafter Srepok), the largest and most remote protected area in the EPL, contained a relatively high number of Leopard, but recent increases in poaching and reported density declines suggest the status of this population might have deteriorated. However, reliable information is lacking on the current population status and long-term trend, which are critical to assess conservation status, determine the effectiveness of current management practices and guide conservation actions. Here, we used open population spatial capture-recapture models to estimate density, survival, per capita recruitment, and population growth rates of the Indochinese Leopard in Srepok using data from 7 systematic camera-trap surveys conducted over 11 years, in the first-ever study of Leopard population dynamics in Asia. Our results showed that during the study period the population (a) declined by over 82%, (b) had low survival probability and low recruitment rates, and (c) is expected to continue declining, suggesting imminent extirpation under unchanged dynamics. The primary reason for the grim situation of the Leopard in Srepok appeared to be the rise in anthropogenic stressors, particularly snaring, which occurred against a backdrop of increased enforcement efforts. Despite the importance of this population, the last decade of management interventions has fallen short of conserving this Critically Endangered Leopard subspecies in the landscape. This has important implications for Leopard conservation in the wider region, notably that efforts should now focus on remaining viable populations, particularly those within the remaining two strongholds of the subspecies: Peninsular Malaysia and the Northern Tenasserim Forest Complex. In protected areas that still harbour Indochinese Leopard, we recommend an improvement of the enforcement strategies, strengthening of the legislation

against poaching, and engagement of local communities to prevent further extirpations. We also advocate for long-term studies in remaining Indochinese Leopard populations throughout the region, to enable timely conservation action and avoid the complete demise of this subspecies.

Key words: Camera trap, long-term monitoring, open population spatial capture-recapture, *Panthera pardus*, population demographics, population dynamics, population viability analysis, Southeast Asia, threatened species monitoring.

6.2 Introduction

Despite its adaptability in habitat use and diet (Hayward *et al.*, 2006, Stein and Hayssen, 2013), the Leopard (*Panthera pardus*) has experienced severe declines in distribution and numbers (Jacobson *et al.*, 2016), leading to its recent uplisting as Vulnerable by the IUCN (Stein *et al.*, 2016). Consequently, the Leopard now occurs in mostly small and fragmented populations, especially in Asia where a disproportionally high range loss (83-87%) has occurred (Jacobson *et al.*, 2016), and where 7 of 8 subspecies are already listed or petitioned to be listed as Endangered or Critically Endangered. Like many large carnivores, the Leopard in Asia has undergone substantial declines in both population size and geographic range, and is at high risk of extinction driven by both its intrinsic biological traits (e.g., low reproductive rates, large ecological requirements) and the ever-increasing anthropogenic pressures. This is particularly true in Southeast Asia, where the accelerated pace of development, infrastructural growth, recent explosion in the illegal wildlife trade, and insatiable global demand of certain products (e.g., palm oil, rubber, cement, timber) are generating unprecedented and increasing pressures on species and entire ecosystems (Hughes, 2017b).

The Critically Endangered Indochinese Leopard (*P. pardus delacouri*), a genetically distinct subspecies, historically occurred throughout all of mainland Southeast Asia and southeastern China (hereafter Indochina; Rostro-García *et al.*, 2016a, Rostro-García *et al.*, 2019). However, populations throughout the region have declined, and this subspecies now occupies only 2-6% of its historical distribution, with surviving populations being fragmented and at low densities (Rostro-García *et al.*, 2016a, Rostro-García *et al.*, 2019). Previous studies have identified 3 priority sites for Indochinese Leopard conservation in Indochina: (i) the Northern Tenasserim Forest Complex on the Thailand–Myanmar border, (ii) Peninsular Malaysia and (iii) eastern Cambodia (Rostro-García *et al.*, 2016a, Rostro-García *et al.*, 2019). In Cambodia, the Indochinese Leopard has declined dramatically, and now occurs only in about 4% of its historical range (Rostro-García *et al.*, 2019). The only potentially viable population remaining in the country occurs in the Eastern Plains Landscape (EPL), a large protected-area complex located in eastern Cambodia (Rostro-García *et al.*, 2019). Because the Leopard is reportedly extirpated from Vietnam and Laos (Rostro-García *et al.*, 2016a, Rostro-García *et al.*, 2019),

the population in the EPL represents the last known viable population in all of eastern Indochina (Cambodia, Laos, Vietnam).

In contrast to most of Indochina, the EPL is dominated by savannah-like habitat (i.e. dry open deciduous forests), and is unique for containing the last remaining population of Indochinese Leopard in which melanism appears to be absent (other populations appear to contain only melanistic Leopard, or a mixture of melanistic and spotted Leopard; Rostro-García *et al.*, 2016a, Rostro-García *et al.*, 2021). Within the EPL, the Leopard reportedly occurs only in two adjacent protected areas: Srepok Wildlife Sanctuary (hereafter Srepok) and Phnom Prich Wildlife Sanctuary (PPWS). In 2009, the Leopard density within Srepok, the larger of the two protected areas, was estimated to be 3.6 individuals/100 km^2 (Gray and Prum, 2012), indicating this landscape likely contained a relatively high number of Leopard. However, recent studies reported a rapid decline in Leopard density in Srepok (Chapter 3, Rostro-García *et al.*, 2018) and low densities within both protected areas (Chapter 3), likely driven by increases in poaching, which already led to the extirpation of Tiger (*Panthera tigris*) in the EPL (O'Kelly *et al.*, 2012). Because of the alarming results reported by these studies and the ever-increasing threats to Leopard survival within the EPL, information on the long-term population trend is needed to assess the conservation status of the species, determine the effectiveness of current management practices, and guide conservation actions. This information is especially important for species such as Leopard, which naturally have low fecundity (Balme *et al.*, 2013) and are exposed to numerous threats owing to their wide ranging movements (Balme *et al.*, 2010b). However, reliable assessments of Leopard population dynamics in Asia are scarce due to the financial and logistical difficulties of conducting these studies at the required temporal and spatial scales. Accordingly, to date no study has yet investigated long-term population dynamics of Leopard in Indochina, which we attribute to a lack of conservation investment on the species in the region.

Although relevant and informative, estimates of state variables (e.g., density, abundance) from single-season or closed population models provide a limited representation in time, allowing for inferences about spatial variation but not temporal dynamics (Karanth *et al.*, 2006). Demographic or vital rates (e.g., recruitment, survival) are essential to understanding the drivers of population dynamics and quantifying population trends through time, and therefore are critical for the conservation of the

target species (Duangchantrasiri *et al.*, 2016, Karanth *et al.*, 2006). Population size and dynamics can directly be estimated through capture-recapture methods (Royle *et al.*, 2014). In classical open population capture-recapture methods, animal movements, particularly of wide ranging species, can make it challenging to distinguish between survival and emigration processes, which in turn can bias the estimates of the demographic parameters (Royle *et al.*, 2014). By explicitly incorporating information on the movement and spatial location of an individual into the model, open population spatial capture-recapture (hereafter open SCR) models address this issue and offer a more realistic representation of the ecological processes (Gardner *et al.*, 2018, Royle *et al.*, 2014, Satter *et al.*, 2019). Despite its advantages, to date only a few published studies have used open SCR models (Augustine *et al.*, 2020, Bischof *et al.*, 2020, Gardner *et al.*, 2010, Gardner *et al.*, 2018, Satter *et al.*, 2019), none of which targeted the Leopard. We used open SCR models to estimate density, survival, per capita recruitment, and population growth rates of the Critically Endangered Indochinese Leopard at a conservation priority site for the subspecies. We used data obtained from 7 systematic camera-trap surveys conducted over 11 years in the first-ever study of Leopard population dynamics in Asia. We predicted that despite increases in enforcement efforts, Leopard density would have continued to decrease in Srepok, owing to the increases in anthropogenic stressors, particularly snaring, in the region. Our results will help determine the effectiveness of management practices and guide conservation efforts for this subspecies.

6.3 Materials and methods

6.3.1 Study area

The study was conducted in Srepok Wildlife Sanctuary (Srepok; 3,730 km^2), formerly called Mondulkiri Protected Forest until 2016, located in the Eastern Plains Landscape (EPL) of Cambodia (Figure 6.1). The habitat of Srepok is dominated (ca. 70%) by open dry deciduous dipterocarp forest in relatively flat terrain, interspersed with small patches of evergreen forests on hill tops and riparian forests along streams and rivers (Rostro-García *et al.*, 2018, Rostro-García *et al.*, 2021). Srepok has a distinct dry season for approximately 6 months (November-April, average monthly rainfall: 3-121 mm), followed by a pronounced rainy season (May-October, average monthly rainfall: 248-370 mm; rainfall

data were from nearby Sen Monorom, Cambodia, 1982-2012; en.climate-data.org/; accessed on 10 July 2019). Elevation ranges from 100 m to 400 m. Large (>15 kg) carnivores present in Srepok during the study period included Dhole (*Cuon alpinus*), and Sun Bear (*Helarctos malayanus*; Rostro-García *et al*., 2018). Smaller carnivores included the Golden Jackal (*Canis aureus*), Indochinese Jungle Cat (*Felis chaus fulvidina*), Leopard Cat (*Prionailurus bengalensis*), Greater Hog Badger (*Arctonyx collaris*), Yellow-throated Marten (*Martes flavigula*), Small Asian Mongoose (*Herpestes javanicus*), Crab-eating Mongoose (*H. urva*), Ferret Badger (*Melogale* spp.), Large Indian Civet (*Viverra zibetha*), Small Indian Civet (*Viverricula indica*), Large-spotted Civet (*Viverra megaspila*), and Asian Palm Civet (*Paradoxurus hermaphroditus*). The wild ungulate community in Srepok is dominated by Banteng (*Bos javanicus*), Northern Red Muntjac (*Muntiacus vaginalis*, hereafter Muntjac), and Wild Boar (*Sus scrofa*), all prey species of the Leopard (Rostro-García *et al.*, 2018). Our research was carried out within the core area (ca. 1,700 km^2), located in the eastern part of Srepok, where human access was restricted (Figure 6.1). Within this area there were no villages or agricultural fields, and livestock grazing was not permitted. Legal human activities within the core area included law enforcement patrols, and research activities. Up until 2018, the collection of non-timber forest products by local people also was allowed in the core area, but starting in 2019 this activity was forbidden when the Royal Government of Cambodia approved the management zonation plan for Srepok. However, illegal human activities such as logging, and poaching occurred in the core area throughout our study. Although no villages occur within the core area of Srepok, several villages occur along the northern, western, and southern borders of Srepok.

6.3.2 Camera trapping

We obtained records of Leopard from 7 systematic camera-trap surveys conducted in Srepok from 2009 to 2019. Camera-trap grids approximated a systematic array, adjusted to the logistical circumstances, to cover parts of the core area of Srepok. Camera-trap stations were set typically for 3 months during the dry season, with an average of 63 stations per year (Table 6.1). In general, each station consisted of a pair of camera traps that operated 24 hours/day, placed on opposite sides of a trail to obtain photos of both flanks of detected individuals. Camera-trap stations were usually spaced 2-3 km apart and

deployed at locations where Leopard signs were found, or places that maximised chances of encountering Leopard (e.g., animal trails, dirt roads, ridges), as carnivores species have been shown to have significantly higher probability of being detected on these landscape features, relative to random placement during the dry season (Cusack *et al.*, 2015, Sollmann *et al.*, 2011). Cameras were placed on trees located 2-3 m from the middle of the trail, and motion detectors set to trigger at a height of 40-45 cm above the centre of the trail. Camera-trap stations were typically checked approximately one month after setting. During these checks, some stations were relocated to nearby locations to reduce risk of theft, flood, or fire. In addition, a few stations were relocated when fresh Leopard sign was found nearby, or if an extremely low detection of mammals occurred in the original location.

We identified Leopard individuals in photographs based on the unique spot patterns, and their sex was determined, when possible, based on the presence of distinctive morphological features (i.e., secondary sexual traits). Because dependent subadults (i.e., those photographed with their presumed mother) are not reliably photographed, these were removed from the analyses. For each detection, the same 2 researchers identified individual animals from the pelage markings. We created a reference collection of two-sided photos for each individual, and for individuals with only single-sided photos, we used the side with the highest number of records to avoid double counting. We note that the 2009 data set overlapped with that used by Gray and Prum (2012) except that we used data from a larger time frame. In some stations, data were not collected for one of the pair of cameras for part of the survey period due to damage caused by fire, humans, or animals. However, we considered a station (i.e., the pair of cameras at each camera-trap location) operational if at least one camera was functional.

Leopard also was known to occur in the adjacent PPWS (2,225 km^2; Rostro-García *et al.*, 2019); thus we also conducted camera-trap surveys for the species in that protected area during 2016, 2018, and 2019, using the same methodology described above. However, the number of Leopard recorded in PPWS was too low to examine population dynamics. Nonetheless, we provide a summary of the Leopard data and camera-trapping efforts in PPWS in Appendix 6.1 (Table A6.1).

6.3.3 Analyses

We fitted hierarchical open SCR models in a Bayesian framework to estimate combined and sex-specific population parameters of Leopard (Chandler and Clark, 2014, Gardner *et al.*, 2010, Satter *et al.*, 2019). Specifically, we aimed to estimate survival probability (φ), per capita recruitment rate (γ), and population growth rate (λ) of Leopard in Srepok over the 11-year period, while accounting for imperfect detection, non-consecutive survey years and home range relocation between primary periods (i.e., years). Because we surveyed the population over non-consecutive primary periods, either a direct estimation of the latent population state (in un-surveyed years) or a scaling of the demographic parameters by the interval between survey years was required (Augustine *et al.*, 2020, Chandler and Clark, 2014, Milleret *et al.*, 2020). Posterior distributions for latent population dynamics that incorporate the uncertainty derived from missing primary period data can be obtained through Bayesian methods (see below; Augustine *et al.*, 2020).

Data structure

We structured our data according to a "robust design" (Pollock, 1982) by considering each year as a primary period and each day within a survey year as a secondary period. The primary period is the unit of time between which demographic changes are assumed to occur. The secondary periods allowed for estimation of yearly closed population abundance in the presence of imperfect detection (Royle *et al.*, 2014, Satter *et al.*, 2019). The detection history was formatted as a three-dimensional array with dimensions $n \times j_{max} \times T$, where n is the total number of Leopard captured across all years, j_{max} is the maximum number of camera traps used in any year, and T is the total number of years of the study.

Process model

We used the density-independent population growth model described by Chandler and Clark (2014), modified for sex specificity of the parameters (Augustine *et al.*, 2020, Satter *et al.*, 2019). The sex-specific parameters of the model were the female- and male-specific survival probabilities (φ^f, φ^m), and per capita recruitment (number of recruits/N; γ^f, γ^m). We denoted total, female, and male

abundance in year *t* as N_t, N_t^f, N_t^m, respectively. Then, the female- and male-specific abundances in years 2,…,*T* were determined by their abundance in the previous year according to $N_{t+1}^f = \varphi^f N_t^f + \gamma^f N_t$ and $N_{t+1}^m = \varphi^m N_t^m + \gamma^m N_t$, with the total abundance in each year being the sum of the sex-specific abundances. The yearly population densities, in turn, were the abundances divided by the area of the state-space (defined below). Associated with each Leopard was its sex, stored in an $1\ x\ n$ vector ***C***, with entries 0 indicating male, 1 indicating female, and missing value indicating individually identified samples where sex could not be determined. Also associated with each Leopard *i* in year *t* were two-dimensional coordinates representing the year-specific activity centres (s_{it}), with the year specificity permitting each Leopard to relocate between years (Augustine *et al.*, 2020, Royle *et al.*, 2014, Satter *et al.*, 2019). We assumed spatial uniformity of activity centres in the first year (Gardner *et al.*, 2018, Satter *et al.*, 2019) across the continuous state-space (*S*), which represented the area in which the population lived, $s_{i,1} \sim Uniform(S)$. We defined *S* by buffering the maximal extent of all traps used (i.e., pooled across years) in the *X* and *Y* dimension by at least four times the estimated detection function spatial scale parameter (σ, see below), resulting in a rectangular *S*. In open SCR models, the specification of the model describing movement of the activity centres between primary periods is one important mechanism to distinguish between emigration and survival (Gardner *et al.*, 2018). The use of appropriate models of individual relocation between primary periods is required to obtain unbiased estimates of population parameters, particularly recruitment and survival (Augustine *et al.*, 2020, Gardner *et al.*, 2018). We assumed a Markovian movement model, where activity centres followed a Gaussian random walk across primary periods (Gardner *et al.*, 2018, Royle *et al.*, 2014, Schaub and Royle, 2014). We believe this to be an ecologically realistic representation of the spatial population dynamics of Leopard in the study area, as individuals likely moved and shifted their activity centres over time due to intrinsic characteristics (e.g., territoriality) and extrinsic factors (e.g., anthropogenic disturbances). To preclude activity centres from leaving the state-space *S*, which defined the spatial domain of the model, we truncated the random walk at the limits of *S*. Specifically, conditional on the location of activity centres in the first year, the activity centres in primary period *t* + 1 were obtained as draw from a bivariate normal distribution centred on the activity centre in primary

period *t* following $s_{i,t+1} \sim Bivariate\ Normal(s_{i,t}, \sigma^T I)$, where $\boldsymbol{I}$ is the identity matrix and σ^T is the year-level spatial scale parameter, which determined how far individuals could relocate. Due to the poor mixing of σ^T, likely owing to the sparsity of the data, we did not consider this parameter to vary by sex. The population and transition dynamics were modelled for all 11 years, with these processes being observed in 7 of those years. In the years when no survey was conducted, the abundance estimates were obtained from the process model by using the information from the estimated population dynamics parameters and the estimated population states in adjacent years with surveys (see Augustine *et al.*, 2020, Chandler and Clark, 2014, and Satter *et al.*, 2019 for previous applications).

Preliminary results of the fully sex-specific model indicated that survival was similar between males and females; thus, and considering the sparsity of the data, we fitted a simplified version of the process model described above but with a single survival parameter for both sexes. We report and discuss the results obtained from this simplified version of the model.

Observation model

During each year *t*, individuals were observed at camera-trap locations X_t over K_t occasions. We recorded observations as binary detection events with a maximum of one detection per camera-trap location per trap day for an individual Leopard and summed detections over occasions. We used a Binomial observation model and assumed the individual trap-by-year number of observations was distributed as $y^c_{i,j,t} \sim Binomial(p^c_{i,j,t}, K_t)$ for $c \in (f, m)$, where $p^c_{i,j,t}$ are the sex-specific individual by trap-by-year capture probabilities. We assumed the capture probabilities were determined by a half-normal detection function conditional on the yearly activity centres, and thus the sex-specific detection probability for individual *i* at trap location *j* in year *t* on each occasion, $\lambda^c_{i,j,t}$, was a decreasing function of the distance between the individual's activity centre s_{it} and a trap location x_j: $\lambda^c_{i,j,t} = \lambda^c_0 exp\left(\frac{\|s_{i,t} - x_{j,t}\|^2}{2(\sigma^c)^2}\right)$, where λ^c_o and σ^c are the sex-specific baseline detection rate and spatial scale parameters, respectively. The observed sexes were stored in vector $\boldsymbol{C}$ of length n_T (total number of Leopard captured across all years), with the possibility that the sex of some individuals was not

observed. We note that we used the Greek letter lambda in three instances: λ for the population growth rate, λ_o^c for the sex-specific baseline detection rate, and $\lambda_{i,j,t}^c$ for the detection rate of individual *i* of sex *c* at trap *j* in year *t*.

Bayesian inference via data augmentation and Markov Chain Monte Carlo (MCMC)

We augmented the three-dimensional capture history containing the detection frequencies to dimension $M \times j_{max} \times T$, where $M = 350$ was chosen to be greater than the expected number of individuals ever alive during the 11-year period. To indicate whether Leopard *i* was in the population in year *t*, we introduced the $M \times T$ matrix $\boldsymbol{z}$, with entries of 1 indicating that the individual was alive and 0 otherwise. We used this matrix to estimate both population size in every year and population dynamics parameters as described by Chandler and Clark (2014). The observed sex vector $\boldsymbol{C}$ also was augmented to length *M*, which was used to estimate the sex of uncaptured and sex-indeterminate individuals (Royle, 2009). We introduced a parameter p^{sex} for the probability that any randomly selected individual was a female and assumed the sex of Leopard *i* was distributed as $sex_i \sim Bernoulli(p^{sex})$. We used custom MCMC algorithms from the *OpenPopSCR* R package (Augustine, 2018), typical vague priors for all population parameters (Chandler and Clark, 2014, Royle *et al.*, 2014, Satter *et al.*, 2019) and sampled from the joint posterior distribution using 20 chains for 250,000 iterations each, thinned by 50, and discarding the first 2,500 iterations of each chain as a burn-in. Posterior samples of yearly sex-specific realized abundances were derived following $N_t^C = \sum_i \left(z_{it} \times I(c_i)\right)$ where I is an indicator function evaluating whether the sex of individual *i* is male (0) or female (1). We also derived combined and sex-specific realized yearly population growth rates from the appropriate abundance, following $\lambda_t = N_t \,/\, N_{t-1}$ and $\lambda_t^C = N_t^c / N_{t-1}^c$ for $c \in (f, m)$ and $t > 1$, and obtained yearly densities by dividing the respective abundance by the area of *S*. We report results as posterior modes and 95% highest posterior density intervals (HPDI).

For each parameter we calculated the Monte Carlo standard error, considering values less than 5% of the posterior standard deviation acceptable, assessed chain convergence using the Gelman-Rubin

statistic, assuming that values $\hat{R} < 1.1$ indicated convergence (Gelman *et al.*, 2004), and visually inspected the trace plots.

Forecasting of population size and assessment of extinction probability

We used the fitted model to extrapolate beyond the study years and obtain abundance projections. We predicted expected population sizes 10 years into the future from the last year of survey (i.e., to 2029). In addition, to more closely reflect the trend in the population under study, we obtained the realized population projection conditional on the posterior of $\boldsymbol{z}$ for the final year of data collection. We generated the predictions by taking as input the posteriors of φ, γ^f, γ^m, p^{sex} from MCMC samples, and simulating new values of $\boldsymbol{z}$ based of the fitted open SCR model for 10 future years. We did this for each iteration of each chain, which were then combined to obtain a posterior distribution for predicted realized abundances. From the population trajectory, we estimated time to and probability of quasi-extinction, defined as the probability that the population size fell below a critical threshold, which we considered at 10 individuals, or if individuals of only 1 sex remained (i.e., population viability analysis [PVA]). We estimated the posterior probability that the realized population size was <10 individuals, and used the posterior mode and 95% HPDI of abundance in the projected years as additional indicatives.

Activity patterns

Previous studies have revealed a strong effect of humans on activity patterns of mammals (Gaynor *et al.*, 2018, Ngoprasert *et al.*, 2017, Ohashi *et al.*, 2013, van Doormaal *et al.*, 2015), including the Leopard (Chapter 3). Therefore, we examined Leopard activity patterns for each survey year separately using non-parametric circular kernel-density functions, where the observed capture times were regarded as random samples from underlying continuous distributions (Ridout and Linkie, 2009), using the R package 'overlap' v.0.3.2 (Meredith and Ridout, 2018). To account for the successive changes of the sun's position throughout the year in the celestial sphere (Nouvellet *et al.*, 2012), we determined sunrise and sunset times based on the location and dates prior to the analysis, and each record mapped so that

sunrise and sunset corresponded to π/2 and 3π/2, respectively. We determined the proportion of the density that occurred between sunrise and sunset.

6.3.4 Law enforcement, species, and illegal incidents

We used data concurrently obtained from the Spatial Monitoring And Reporting Tool (SMART: https://smartconservationtools.org/), designed to measure, evaluate and improve the effectiveness of wildlife law enforcement patrols and site-based conservation actions. We extracted the geolocations of law enforcement incidents of illegal activity (e.g., logging, snaring) detected and recorded by enforcement units during patrolling sessions conducted in Srepok from January 2009 to December 2019. We also gathered information about enforcement efforts carried out throughout the years, including number of rangers, kilometres patrolled, and number of lethal traps (e.g., snares, metal snap traps) removed. We calculated lethal trap encounter rate as the number of lethal traps encountered per 100 km patrolled. Data from SMART and enforcement efforts was also gathered for PPWS (Table A6.2).

Given that data collection is not the primary objective of the enforcement units, ranger-collected data may be subject to considerable bias and should thus be treated with caution to avoid misleading conclusions (Ibbett *et al.*, 2020b, Keane *et al.*, 2011). In addition, SMART records may not represent an accurate index of density of threats (e.g., snares) per year due to the variability in detection rate that arises from differences in effort (e.g., patrol focus, strategy, coverage). Therefore, we also calculated the detection frequencies (DF) of human-related events and mammal species >2 kg for the first and last survey as proxies of anthropogenic pressures and their potential effects on mammal species. Although there is a high diversity of small mammal, reptile, and bird species in the study area, some of which were recorded during the surveys, we considered mammals >2 kg due to camera placement (i.e., height of 40-45 cm above in trails) and sensitivity settings (i.e., moderate sensitivity), which likely precluded many species <2 kg from being detected reliably. Human-related events included records of illegal anthropogenic activities (e.g., logging, poaching), as well as records of domestic animals (i.e., dogs and cattle), which typically were accompanied by illegal intruders in our study area. We excluded photographs of researchers and park staff, which, although they may have

temporally caused disturbances, were not associated with major anthropogenic stressors. We defined the DF as the number of notionally independent photographs of each species divided by total camera trap days multiplied by 100. We considered independent events as photographs of the same species taken >60 minutes apart at the same station to avoid inflated counts caused by repeated detections of the same event. Although in most cases the DF might not be unambiguously attributed to actual differences in abundance due to the effects of diverse confounding factors (e.g., movement patterns, camera-trap set up, station selection criteria; Sollmann, 2018), we assumed that differences in DF were associated with differences in abundance given that the same area was surveyed, and cameras were placed along the same roads using similar methodologies.

6.4 Results

The 7 surveys conducted across 11 years yielded detections of 35 adult Leopards (19 females, 8 males, 8 unknown sex) over 29,756 trap nights from 441 camera-trap stations (Table 6.1). The number of unique individuals detected in any given survey year varied threefold, with the number of recaptures for a given individual within a survey ranging from 0 to 54. Notably, the number of individuals detected declined over the years, from 12 individuals in the first survey (2009) to 4 in the last survey (2019; Table 6.1). In accordance, the total number of Leopard detections per year decreased dramatically from the first survey (n = 123) to the last survey (n = 24). Similarly, the percentage of cameras that detected Leopard decreased 75% from 2009 to 2019 (Table 6.1). The number of adult males detected declined over the years, with the last 2 surveys consisting exclusively of females (Table 6.1). The proportion of Leopard records that occurred during daylight declined throughout the study, ranging from 49% in the first survey to only 8% in the last survey.

The annual survival probability point estimate was 0.58 (95% HPDI: 0.42-0.70, Table 6.2), indicating the death of about 42% of all individuals per year. Annual per capita recruitment rates were low (<0.25) and estimated to be 86% larger for females than males (Table 6.2). The yearly expected population growth rates, implied by the per capita recruitment and survival estimates, indicated a decline in the population (Figure 6.2). The population density declined 82% from an estimated 1.5 (1.0-2.4) to 0.3 (0.1-0.5) Leopard/100 km^2 across the 11 years (Figure 6.3), with no overlap of the 95%

HPDI between the first and last survey. Female density estimates were higher than those of males during all years (Figure 6.3). Accordingly, estimates of the yearly realized sex ratio indicated a female bias over the study period, with the 95% HPDI not overlapping 0.5 (i.e., equal sex ratio). The detection probability varied by sex, with males being more detectable at their activity centre than females ($\hat{\lambda}_0^m$ = 0.03; 0.03-0.04; $\hat{\lambda}_0^f$ = 0.02; 0.02-0.03), and the within-year detection function spatial scale parameter (σ) being 1.84 times larger for males ($\hat{\sigma}^m$ = 4.60 km, 4.18-5.20 km) than for females ($\hat{\sigma}^f$ = 2.51 km, 2.28-2.83 km; Table 6.2). The pooled-sex activity centre relocation spatial scale parameter (σ^T) was 4.88 km (3.34-7.48 km) and could scarcely be estimated (i.e., low effective sample size) given the sparsity of the data. However, the pairwise correlations of posterior samples for this parameter and survival, female- and male-specific recruitment were low (0.20, -0.21, -0.13, respectively; Figure A6.1), indicating little influence of the specific numerical value of σ^T (i.e., range covered in the posterior) on estimates of the demographic parameters.

Realized population growth rates over the entire 11-year period were estimated at 0.14 (0.06-0.33) overall, and 0.16 (0.06-0.40) for females. The annual realized population growth rate assuming constant growth over time were 0.84 (0.77-0.91) overall, and 0.85 (0.77-0.93) for females (no sensible estimate could be obtained for males due to extinctions in some MCMC draws; see below). Using the estimated realized population growth rates over the entire 11-year period, the posterior probability that the overall, and female population was declining ($\lambda<1$) was 1.00 in both cases. The posterior probability that the overall, and female population was declining by more than 25% each year ($\lambda<0.75$) was 1.00 in both cases. Realized population growth rates for males were not calculated because the population dropped to 0 in several iterations, particularly during the last 2 surveys where the probability that males were extinct was 0.22 and 0.27, respectively.

Considering the estimates of survival and per capita recruitment, the associated expected abundances during the years predicted into the future indicated a further decline of the population trajectory (Figure 6.4). Similarly, the realized population projection indicated a decline of the population (Figure 6.5), with the first population estimate below 10 individuals occurring in 2021 (9.88, 95% HPDI: 1-24). Our simple PVA based on the fitted population model suggested that the probability

that the population would fall below 10 individuals in 10 years from the last survey (i.e., in 2029) was 89%.

In the adjacent PPWS, the number of Leopard recorded in 3 surveys conducted across 4 years (2016-2019) declined from 5 individuals to 2 individuals, and the detection frequencies of Leopard declined at a similar rate (Table A6.1).

6.4.1 Law enforcement, species, and illegal incidents

Enforcement efforts in the area increased over the 11-year survey period, particularly during the last 2 years with over 60% increase in distance patrolled compared to the first survey year and over 90% compared to the year with the smallest distance patrolled over the 11-year period (i.e., 2012; Table 6.3). Similarly, the number of rangers doubled between the first and last survey, the latter of which had almost 4 times more rangers compared to the year with the least number of rangers (i.e., 2014; Table 6.3). In contrast, the number of illegal incidents recorded by the enforcement teams and camera traps increased over time even when standardized by effort. The encounter rate of lethal traps (e.g., snares, metal snap traps) removed in Srepok increased about 500-fold from the first to the last survey (Table 6.3), being much higher during the second half of the study period (Figure 6.6). Human-related events detected by camera traps considerably increased from 2009 to 2019, with a more than 20-fold increase in detection frequencies (Table A6.3). Conversely, the number of mammal species photographed decreased over the study period. Although the number of detected mammal species >2 kg appeared to be similar between 2009 and 2019, there were two mammal species that were not detected in 2019 but that were detected in 2009, Greater Hog Badger and Sun Bear. In addition, the DF of larger species (e.g., Banteng, Gaur) declined over time, whereas the DF of some of the smallest or common species (e.g., Wild Boar, Golden Jackal, Burmese Hare *Lepus peguensis*) increased over time (Table A6.3).

6.5 Discussion

By applying open SCR models to an Indochinese Leopard camera-trapping data set spanning 11 years, we were able to estimate population demographic parameters, which provided us with a better picture of the population status and trend of this Critically Endangered subspecies in a conservation priority

site. To our knowledge, this is the first study to use open SCR models on a Leopard population, and the first long-term study to investigate population dynamics of the species in Asia. Alarmingly, our findings suggest an extremely grim situation of the Leopard by showing that (a) individuals had a low survival probability and low recruitment rates, (b) the population declined by 82% over 11 years, and (c) the population trajectory is expected to continue declining and suggests that extirpation is imminent.

The estimated survival probability was low and indicated the loss of about 42% of all individuals, and thus an estimated turnover of almost half of the population per year. Similarly, per capita recruitment rates were low, and indicated that male recruitment was lower than female recruitment. Because we provided the first estimates of per capita recruitment for Leopard, we are unable to compare our estimates to previous studies. Nevertheless, we hypothesized that higher female recruitment could be due to sex-specific dispersal and survival to adulthood. Leopard females tend to exhibit philopatry and typically have smaller home ranges than sympatric males (Balme *et al.*, 2017c, Fattebert *et al.*, 2015). In contrast, males tend to disperse further, and range over larger areas compared to females, exposing males to greater anthropogenic risks (e.g., higher chance of being caught in a lethal trap when moving through its territory, and more likely to wander near the protected area boundaries where anthropogenic pressures are greater). Indeed, the activity centres of recaptured individuals suggested that female Leopard were mostly philopatric in Srepok. Alternatively, higher female recruitment may be partially explained by an uneven sex ratio at birth or the skewed sex ratios typical of mammalian populations which tend to become more female-biased among adults due to physiological, genetical, and behavioural differences (Mills, 2012). Although the preliminary sex-specific model did not reflect any differences in survival probability between the sexes, it is likely that we had insufficient data for males to draw stronger inferences. However, we suspect a higher mortality of males, owing to the inverse relationship between survival and dispersal distance (Bonte *et al.*, 2012), which in turn presumably caused the lower male recruitment and skewed sex ratios observed. Previous studies have reported that anthropogenic disturbances, including increased human access to protected areas, can decrease recruitment in carnivores (Ausband *et al.*, 2015, Broekhuis, 2018, Kerley *et al.*, 2002). Importantly, the Leopard population in Srepok likely was particularly sensitive to mortalities as there appears to be sub-optimal connectivity with the neighbouring subpopulation in adjacent PPWS,

making compensation by immigrants unlikely. This, in conjunction with the unsustainable mortality rates, can further impact the population health and viability by disrupting natal dispersal mechanisms of the remaining individuals and compromising outbreeding behaviour and gene flow (Naude *et al.*, 2020a).

To date only a few studies have investigated Leopard population trends over >3 years; most of which have been conducted in southern Africa where both ecological and anthropogenic circumstances are considerably different from those in Indochina. For instance, unlike the precipitous density decline observed in Srepok, the Leopard population in Phinda Private Game Reserve, South Africa, was reported to have increased 56% in a 4-year period due to management interventions (Balme *et al.*, 2009). The only relatively comparable study, conducted in the Soutpansberg Mountains of South Africa, reported a 66% decline in Leopard density from 2008 to 2016 (Williams *et al.*, 2017). However, to our knowledge, the density decline observed during our study is the largest ever documented for the species. Although we predicted a decrease, we did not expect such a steep decline and an imminent extirpation, particularly considering the increases in law enforcement efforts. The dramatic density decline suggests this Leopard population currently is well below potential carrying capacity, particularly considering the habitat and prey available. Ecologically similar sites in dry deciduous forests in India and Nepal have reported Leopard densities ranging from 4-13 individuals/100 km^2 (Kalle *et al.*, 2011, Mondal *et al.*, 2012a, Thapa *et al.*, 2014), or about 20-65 times higher than the density we estimated at the end of our study. It is unlikely that changes in abundance found during our study were caused by differences in methodologies because during most years we surveyed approximately the same area of the inner core of Srepok, the most inaccessible and remote part of the park, using the same methods and study design. Similarly, it is unlikely that the differences were caused by insufficient prey numbers, as the detection frequencies of Muntjac and Wild Boar, preferred and accessible prey of the Leopard in Srepok (Rostro-García *et al.*, 2018), remained relatively stable or increased in the inner core of Srepok from the first to the last survey (2009 to 2019; Table A6.3). Furthermore, line-transect surveys carried out from 2010 to 2018 by WWF Cambodia in the core area of Srepok showed that Wild Boar densities remained stable, whereas Muntjac densities decreased (Groenenberg *et al.*, 2020). However, the decline on Muntjac densities only started to become apparent

in 2016 (Groenenberg *et al.*, 2020), by which time the Leopard population had already declined about 70% from 2009. Therefore, prey numbers likely were sufficient to sustain the Leopard population in Srepok, particularly considering the adaptability in feeding behaviour of the species in this area (Rostro-García *et al.*, 2018). The Leopard population in Srepok was likely more susceptible to snaring than the sympatric ungulates because the Leopard had a lower initial population size, lower intrinsic growth rate, and wider ranging movements, which made the species more sensitive to human-caused mortalities when compared to ungulates (Kragt *et al.*, 2020).

The primary cause for the precipitous decline of the Leopard population in Srepok appears to be the dramatic increase in anthropogenic pressures, notably poaching. Correspondingly, the camera-trap data showed that there was a drastic increase in human activity over the study period, with a 20-fold increase in detection frequencies of human-related events between the first and last surveys (Table A6.3). With the depletion of wildlife in China and Vietnam, poaching has intensified in Cambodia (Harrison *et al.*, 2016), predominantly fuelled by the illegal wildlife trade and the unsatiable demand for wildlife meat, parts, and products. Although poaching is difficult to detect, and suffers from imperfect and varying detection (e.g., based on patrolling effort and strategy, skills of patrolling teams; Ibbett *et al.*, 2020b, O'Kelly *et al.*, 2018), the number of lethal traps clearly increased over the years in Srepok, from being rarely detected at the beginning of the study, to a 500-fold increase in encounter rate by the end of our study (Figure 6.6). This dramatic increase in lethal trap encounter rate happened against a backdrop of increased number of rangers and increased patrolling distances that occurred in Srepok during our study (Table 6.3). Alarmingly, the reported numbers of snares likely was a vast underrepresentation of the reality on the ground, as up to 80% of snares can remain undetected by rangers (Ibbett *et al.*, 2020b, O'Kelly *et al.*, 2018). The increase in anthropogenic disturbances likely explains the shift in Leopard activity patterns from cathemeral to nocturnal during the study period. Previous research has revealed a strong effect of humans on daily activity patterns of mammals (Gaynor *et al.*, 2018). Similarly, the Leopard was shown to become more nocturnal when human activity increased within a protected area of Thailand (Ngoprasert *et al.*, 2017), and the same was likely true for Leopard in Srepok. Thus, our results suggest that humans not only negatively impacted Leopard density but also its activity patterns. In the adjacent PPWS, the patterns were similar to Srepok: number of

Leopard and overall Leopard detections substantially decreased across a 4-year period, during which the number of lethal traps detected by rangers in PPWS rose dramatically despite increases in enforcement effort (Table A6.2, Figure A6.2).

One of the major drivers of poaching in eastern Indochina (Cambodia, Laos, Vietnam) is the high demand for wildlife meat, often regarded as a delicacy or a status symbol, by middle- and upper-class urban consumers (Drury, 2011, Sandalj *et al.*, 2016, Shairp *et al.*, 2016). Cambodia has a high prevalence of poaching and reliance on wildmeat, with an estimated 83% of rural households engaged in wildmeat harvesting at least once per year (Nielsen *et al.*, 2018), including in the EPL (Ibbett *et al.*, 2020a). Multi-species indiscriminate snaring is the most common method used in eastern Indochina, where large numbers of snares are set to capture animals for the commercial wildmeat trade. Snares, usually made from cable, nylon or wire, are affordable and easy to set, but highly damaging to vertebrates due to their indiscriminate nature with respects to species, sex or age (Gray *et al.*, 2018), representing a direct and persistent threat to wildlife as they remain operational in the landscape till retrieved (Ibbett *et al.*, 2020b, O'Kelly *et al.*, 2018). Rare, slow breeding species, with low initial population sizes but high probability of being captured by a snare, such as Tiger and Leopard, are particularly sensitive to snares and can go extinct even when patrolling effort is high (Kragt *et al.*, 2020). Accordingly, widespread snaring has been identified as the main culprit behind Tiger density declines in Southeast Asia (Belecky and Gray, 2020), and their extirpation from eastern Indochina (Johnson *et al.*, 2016, O'Kelly *et al.*, 2012, Rasphone *et al.*, 2019). Although direct evidence of Leopard poaching was scant, the bones and skin of at least one Leopard poached in Srepok were confiscated in 2010 (Gray, 2013), and several unofficial reports of additional Leopards poached in Srepok and adjacent areas were made by local people during our study (authors pers. obs.). It is likely that other instances of Leopard poaching remained undetected as any captured individual likely was rapidly traded across the border to Vietnam where demand is high, and where Leopard was 1 of 13 most common species offered in wildlife restaurants (Anh and Wyatt, 2013). Alongside the rise in wildmeat demand, the unprecedented levels of poaching, particularly snaring, likely were induced by a plethora of interrelated drivers, including increases in illegal logging, and infrastructure development in eastern Cambodia.

Cambodia suffers from extremely high rates of deforestation, the greatest (>47,500 km^2) at the country scale reported during a 20-year period for Indochina (Lohani *et al.*, 2020, Namkhan *et al.*, 2021) and one of the greatest in the world (Heino *et al.*, 2015, Hughes, 2017b). Both Srepok and PPWS experienced severe pressures from illegal logging for luxury timber, as well as both small- and industrial-scale forest clearance associated with farms and Economic Land Concessions granted by the government within the protected area boundaries (Mahanty and Milne, 2016, Riggs *et al.*, 2018). Although the Leopard is a habitat generalist (Rostro-García *et al.*, 2019) and there was no large-scale clearcutting in the core zones of Srepok or PPWS, illegal logging inadvertently led to increased accessibility to these areas, which facilitated the influx of illegal intruders into the core areas, and substantially contributed to the change of poaching from subsistence to commercial level. These pressures were further aggravated in Srepok, which by virtue of being located along an international border, and having a more open, flat, and accessible terrain than other areas within the EPL, was exposed to higher anthropogenic pressures. Consequently, alongside the stressors imposed by locals, illegal activities in Srepok, notably poaching, also were undertaken by Vietnamese nationals, poaching gangs, and military or border police personnel armed with high-powered rifles, all of which were increasingly observed or photographed in the core area of Srepok during the study. The rampant deforestation, rapid acceleration and intensification of poaching, and ubiquity of human-associated stressors in the EPL, likely were catalysed by the infrastructural development of the province. This included improved cellular communication and expanding road networks, which facilitated not only access to previously inaccessible areas, such as the inner core of Srepok, but strengthened trade links (e.g., cross-border) and market integration at local, provincial and regional levels (e.g., Vietnamese markets; Mahanty and Milne, 2016). For example, the paving in 2016 of a major highway (i.e., the National Route 76), which cuts through the western part of Srepok (Figure 6.1), likely acted as a major disturbance in the landscape that facilitated illegal trade from Srepok and adjoining areas. Coincidentally, there was a peak in lethal trap encounter rate in both Srepok and PPWS in 2016. The detrimental effects on wildlife caused by unregulated infrastructural developments likely were further exacerbated by the porous legal frameworks, insufficient law enforcement, and rapid socio-economic growth of the province (Groenenberg *et al.*, 2020).

Although decades of armed conflict and illegal hunting led to the decimation, extirpation, and extinction of some of the diverse and abundant wildlife that historically occurred in the EPL (e.g., Tiger and Kouprey *Bos sauveli*), this complex still contained one of the most intact fauna assemblages of the region at the time our study commenced (Gray *et al.*, 2012a, Gray *et al.*, 2012b, Gray *et al.*, 2014a, Gray and Prum, 2012, Ibbett *et al.*, 2020b). However, evidence from the camera-trap data suggests not only Leopard but other wildlife numbers were decimated throughout the landscape, most plausibly attributable to the proliferation in snaring. For instance, the DF of all large (>15 kg) and some medium-sized (5-15 kg) species in Srepok decreased substantially during our study. In fact, Sun Bear and Hog Badger, both reported to be especially sensitive to snaring (Duckworth *et al.*, 2016, Scotson *et al.*, 2018), decreased throughout the study and were not detected during the last survey (Table A6.3). The decrease in ungulates numbers recently found in both Srepok and PPWS provides further evidence about the damages to wildlife caused by snares and other poaching methods. For example, by 2020 ungulate densities and biomass in both Srepok and PPWS were much lower than those of ecologically comparable sites in South Asia and Indochina, suggesting that ungulate populations currently are severely depleted in both protected areas (Groenenberg *et al.*, 2020). Alarmingly, current Leopard and ungulate densities in Srepok and PPWS are similar to or higher than other areas within the EPL (e.g., Keo Seima Wildlife Sanctuary, Yok Don National Park; Groenenberg *et al.*, 2020), depicting a dire picture for wildlife in the wider landscape.

The EPL, previously heralded as the 'Serengeti of Asia' (Wharton, 1957), supports one of the largest forest tracts of threatened dry deciduous forest remaining in Indochina, and harbours significant populations of wildlife, several of which are threatened, including the largest global population of endangered Banteng, one of the largest populations of the Critically Endangered Siamese Crocodile (*Crocodylus siamensis*), the main stronghold of the Indochinese Jungle Cat, and the largest population of Asian Elephants (*Elephas maximus*) in the country (Daltry *et al.*, 2015, Gray *et al.*, 2012a, Gray *et al.*, 2014a, Rostro-García *et al.*, 2021). The EPL also contains important populations of the Critically Endangered Giant Ibis (*Thaumatibis gigantea*), Endangered Eld's Deer and Dhole, as well as populations of other Threatened carnivores, ungulates, primates, and birds (Gray *et al.*, 2012c, Kamler *et al.*, 2020, Loveridge and Ty, 2015, Pollard *et al.*, 2007). Clearly, if the rates of snaring, illegal

logging, and infrastructure development continue to increase, then these could have implications beyond the study area and Leopard population studied here by compromising the persistence of the remaining globally important wildlife populations. Although Cambodia has more protected areas than any other Indochinese country (UNEP-WCMC, 2021), with 34% of terrestrial land surface under protected status (Souter *et al.*, 2016), several of the protected areas in the country, including Srepok, are becoming devoid of all but the smallest or most common species; and are thus suffering from the already widespread empty forest syndrome (Harrison, 2011, Ibbett *et al.*, 2020a). This is due to protected areas essentially being chronically under-enforced and under-funded, and where overexploitation of natural resources is a pervasive and expanding threat (Ibbett *et al.*, 2020a, Souter *et al.*, 2016). Therefore, to avoid irreparable biodiversity losses it is vital that direct management interventions are taken to restore and protect the remaining wildlife populations in the EPL.

6.5.1 Study limitations

Because information about reproductive behaviour (e.g., birthing months) of wild Indochinese Leopard is unavailable, it is difficult to ascertain population closure over the course of an annual survey. In addition, no specific population closure test for SCR models is currently available (Royle *et al.*, 2014); thus, the time frame that adequately approximates a closed population of Leopard was difficult to estimate. Consequently, on some of our secondary samples the demographic closure assumption might have been violated, particularly in 2014 and 2017 when surveys followed a sequential configuration of the camera traps, and thus lasted longer than 90 days. This in turn might have resulted in an overestimate of the yearly abundance estimates of the years with longer surveys, notably the survey conducted in 2017, which exceeded the maximum number of occasions thus far evaluated as appropriate for the species (Hedges *et al.*, 2015). However, this should not significantly affect the estimation of survival or recruitment rates, nor the overall trend observed and projected for the population. Although during most years we surveyed approximately the same area, which targeted the inner core of Srepok (i.e., the most inaccessible and remote part of the core area), the survey area considerably varied in 2010 and 2018. The latter covered most of the core area, whereas the former was an opportunistic survey with few stations, which likely affected the estimates of that year by reducing the number of individuals

exposed to potential capture as well as of spatial recaptures. Nonetheless, this should not greatly affect the estimation of the dynamic parameters or the overall trend.

The assumption of uniform density may not be appropriate because an edge effect was suspected to be influencing Leopard density in Srepok, likely resulting in a non-homogeneous distribution of the individuals, which we were unable to fully capture due to the higher theft rate of cameras in areas near the border of Srepok. Similarly, the prior assumptions of uniformity may not be adequate because we did not capture the majority of individuals in the state-space, particularly during the first surveys, as evidenced by the ratio of detected individuals to estimates of realized abundance. Consequently, the uniformity assumptions with respects to population dynamics and spatial distribution likely carried more weight. Thus, the estimated density likely was higher than the average density across the state-space. However, the lack of appropriate landscape covariates that could describe the presumed edge effect as well as the scarce data precluded us from using a model for a heterogenous density.

Although we did not detect any major differences in survival between females and males, it is possible that we did not have enough statistical power to detect meaningful differences given the sparsity of the data. Similarly, we were unable to evaluate temporal variation in demographic rates or reflect possible Allee effects due to the sparse data sets, which in turn likely resulted in underestimates of extinction probability, by assuming constant survival and per capita recruitment when in reality these likely declined through time.

6.5.2 Technical recommendations

The practicality and wide adoption of camera traps, together with the ever-increasing technological developments, likely will allow more studies to collect data over larger time periods. With these advances should come parallel improvements in the approaches used to analyse such data. Open SCR models represent a favourable and flexible framework for assessing and monitoring wildlife populations, by explicitly incorporating individual movement in survival estimation and efficiently utilizing available data (Gardner *et al.*, 2018). In addition, the use of a hierarchical Bayesian open SCR model allowed us to better distinguish emigration from survival using an ecologically realistic approach, while also estimating population demographic parameters with greater precision than short-

term studies, including during years when surveys were not conducted. Although further refinements are required, we evidenced the benefits of using open SCR models and recommend their use whenever population dynamics are of interest, and to gather relevant information, such as spatio-temporal patterns of survival and movement of the target species. This information is crucial to understanding and conserving populations in a world that is changing at an increasingly rapid rate. When available, supplementing camera-trap data with additional information (e.g., telemetry data) can be advantageous as it provides information on the location of individuals, and thus may improve the ability to model between-year movements (Gardner *et al.*, 2018).

6.5.3 Conservation implications

Our results indicate that law enforcement efforts were inadequate to tackle the threat posed by poaching, and thus to curtail the imminent extirpation of Leopard and possibly other wildlife from the landscape. Notably, the levels of snaring, which have increased by at least two orders of magnitude during the 11-year study, have surpassed all enforcement efforts to reduce this threat at a landscape level. Therefore, our findings suggest that increases in patrolling effort (e.g., snare removal, patrol distances) alone are unlikely to prevent the imminent local extirpation of Leopard and other wildlife from Srepok and EPL. Similar situations have occurred in other protected areas of eastern Indochina. For example, increases in law enforcement funding and effort in Nam Et-Phou Louey National Protected Area in Laos, were insufficient to prevent the proliferation in snaring, which ultimately caused the recent extirpation of Tiger (Johnson *et al.*, 2016, Rasphone *et al.*, 2019). Efforts to save the Critically Endangered Saola (*Pseudoryx nghetinhensis*) resulted in the removal of >75,000 snares from protected areas in Vietnam, yet levels of snaring remained so high that instead of increased funding for law enforcement and snare removal, the IUCN recommended captive breeding to save the species (IUCN, 2016). Therefore, it is apparent that, unlike in other areas (Linkie *et al.*, 2015), increases in law enforcement efforts alone often are unable to protect wildlife and prevent the proliferation of snaring in eastern Indochina. Although intensified, more efficient, and data-informed patrolling schemes are required, new approaches are undoubtedly needed to protect threatened species within protected areas of this region, where over 12 million snares are estimated to be present (Belecky and Gray, 2020, Kragt *et al.*, 2020).

Importantly, protected areas need to be managed to ensure they truly represent areas optimally free of human disturbances. For that, enforced compliance mechanisms are required, including strengthening of the judicial system, with legislative reforms that criminalize non-traditional, commercialized poaching and possession of snares (including materials to build them), as well as the effective prosecution of offenders and adherence to the penalties proscribed by law (Belecky and Gray, 2020, Gray *et al.*, 2021, Gray *et al.*, 2018, Macdonald *et al.*, 2021). In addition, a better regulation of economic development schemes is needed to mitigate their negative impacts within and around protected areas. Critically, the engagement of local people is essential to reduce snaring and other illegal activities within protected areas of the region. To better understand and reduce the demand dynamics, intelligence-gathering operations that assess commodity chains are required (Ibbett *et al.*, 2020a). Because most snaring is motivated by financial gain (MacMillan and Nguyen, 2014) and driven by the high demand for wildmeat, demand reduction efforts (e.g., social marketing, evidence-based behaviour change interventions) are required to reduce consumption of wildmeat and other wildlife products by the general public. The success combatting the illegal wildmeat and wildlife trade, and ultimately protecting species in eastern Indochina will necessitate strengthening of international legal cooperation to disrupt and dismantle wildlife trafficking in the region (Jiao *et al.*, 2021), as well as commitments and support from all governmental levels, non-governmental organisations, and society.

Regrettably, the population status and trajectory of this Critically Endangered Leopard subspecies suggest that a population recovery in this priority site is unlikely to occur. Despite the regional importance of this population, the last decade of management interventions clearly has fallen short of conserving Leopard in the landscape, similar to what happened with the recently extirpated Tiger. This has important implications for Leopard conservation in the wider region, notably that efforts should now focus on remaining viable populations, particularly those within the two remaining strongholds of the subspecies (i.e., Peninsular Malaysia, and the Northern Tenasserim Forest Complex; Rostro-García *et al.*, 2016a). We advocate for long-term studies of the Indochinese Leopard in the few remaining populations, to enable timely conservation action and avoid their demise elsewhere. Only through the halt of anthropogenic pressures in remaining populations, particularly snaring, and the

urgent, committed implementation of effective strategies can the Leopard have any chance of persisting in a human-dominated Indochina.

6.6 Acknowledgments

We would like to thank collaborating organisations, including WWF Cambodia, Ministry of Environment, and Forestry Administration-Ministry of Agriculture, Forestry, and Fisheries, and their departments in Mondulkiri province (Royal Government of Cambodia). We gratefully acknowledge the support in the field provided by Srepok and PPWS rangers. Funding for field work was provided by Panthera, while SR-G's analyses and writing was supported by a Foley-Béjar Scholarship, provided by Balliol College, University of Oxford, and a grant to DWM from the Turner-Kirk Foundation.

Table 6.1 Summary of Indochinese Leopard (*Panthera pardus delacouri*) camera-trap surveys conducted from 2009 to 2019 in Srepok Wildlife Sanctuary, Cambodia. Trap nights represent the total number of days across all functional (at least 1 operating camera of a pair) camera-trap stations. F = female, M = male, U = unknown.

Year	Trap nights	No. camera-trap stations	Stations detected	Total no. detections	Mean number of detections (range)	Individuals captured (F, M, U)	Cumulative no. individuals detected
2009	3,362	56	38 (67.9%)	123	10.3 (1-55)	12 (7, 5, 0)	12
2010	902	13	8 (61.5%)	23	2.3 (1-6)	10 (5, 3, 2)	17
2014	2,191	43	13 (30.2%)	24	3.0 (1-12)	8 (2, 2, 4)	24
2016	2,973	46	13 (28.3%)	23	3.8 (1-11)	6 (3, 2, 1)	30
2017	4,314	51	11 (21.6%)	28	5.6 (1-15)	5 (3, 1, 1)	32
2018	11,612	163	25 (15.3%)	59	9.8 (1-25)	6 (6, 0, 0)	35
2019	4,402	69	12 (17.4%)	24	6.0 (2-10)	4 (4, 0, 0)	35
Total	**29,756**	**441**	**120 (27.2%)**	**304**	**-**	**35 (19, 8, 8)**	**35**

Table 6.2 Posterior summaries (mode [Estimate], standard deviation [SD]) for the detection and population dynamics parameters obtained using an open population spatial capture-recapture model fitted to camera-trap data of Indochinese Leopard (*Panthera pardus delacouri*) from Srepok Wildlife Sanctuary over 11 years (2009-2019), with data collected in 7 of those years. The 95% credible interval limits (95% CI) provide the lower and upper limits from 95% highest posterior density intervals. λ_0 = baseline detection rate, σ = detection function spatial scale parameter, γ = per capita recruitment rate, φ = yearly survival probability; σ^T = pooled-sex activity centre relocation spatial scale parameter. Superscripts *f* and *m* denote estimates for females and males, respectively.

Parameter	Estimate	SD	95% CI
λ_0^m	0.032	0.004	(0.025-0.041)
λ_0^f	0.020	0.003	(0.015-0.026)
σ^m	4.596	0.266	(4.175-5.203)
σ^f	2.513	0.141	(2.281-2.832)
γ^m	0.035	0.025	(0.004-0.091)
γ^f	0.241	0.063	(0.121-0.365)
φ	0.582	0.070	(0.423-0.696)
σ^T	4.883	1.098	(3.335-7.477)
λ_0^m	0.032	0.004	(0.025-0.041)
λ_0^f	0.020	0.003	(0.015-0.026)

Table 6.3 Enforcement efforts deployed over 11 years (2009-2019) in Srepok Wildlife Sanctuary, Cambodia. Data on distance patrolled and absolute number of lethal traps (e.g., snares and metal snap traps) were obtained from the Spatial Monitoring And Reporting Tool (SMART) and reported by rangers. The encounter rate was calculated as the number of lethal traps encountered per 100 km patrolled.

Year[a]	Number of Rangers[b]	Distance patrolled (km)	Number of lethal traps	Encounter rate
2009	39	19,082	2	0.01
2010	42	31,004	13	0.04
2011	35	27,964	86	0.31
2012	33	4,207	0	0.00
2013	49	25,538	254	0.99
2014	21	23,789	556	2.34
2015	23	32,020	1,883	5.88
2016	45	39,487	3,794[c]	9.61
2017	38	54,646	1,276[d]	2.34
2018	75	42,809	2,105	4.92
2019	80	58,977	2,634	4.47

[a] information, available from monthly reports, considers yearly data 10 Dec-10 Dec instead of calendar years

[b] includes Ministry of Environment rangers, police rangers, army rangers, and community rangers. Recruitment of community rangers started in 2017.

[c] intensive targeted snare sweeping campaign implemented by WWF Cambodia and the Ministry of Environment.

[d] enforcement efforts focused on illegal logging.

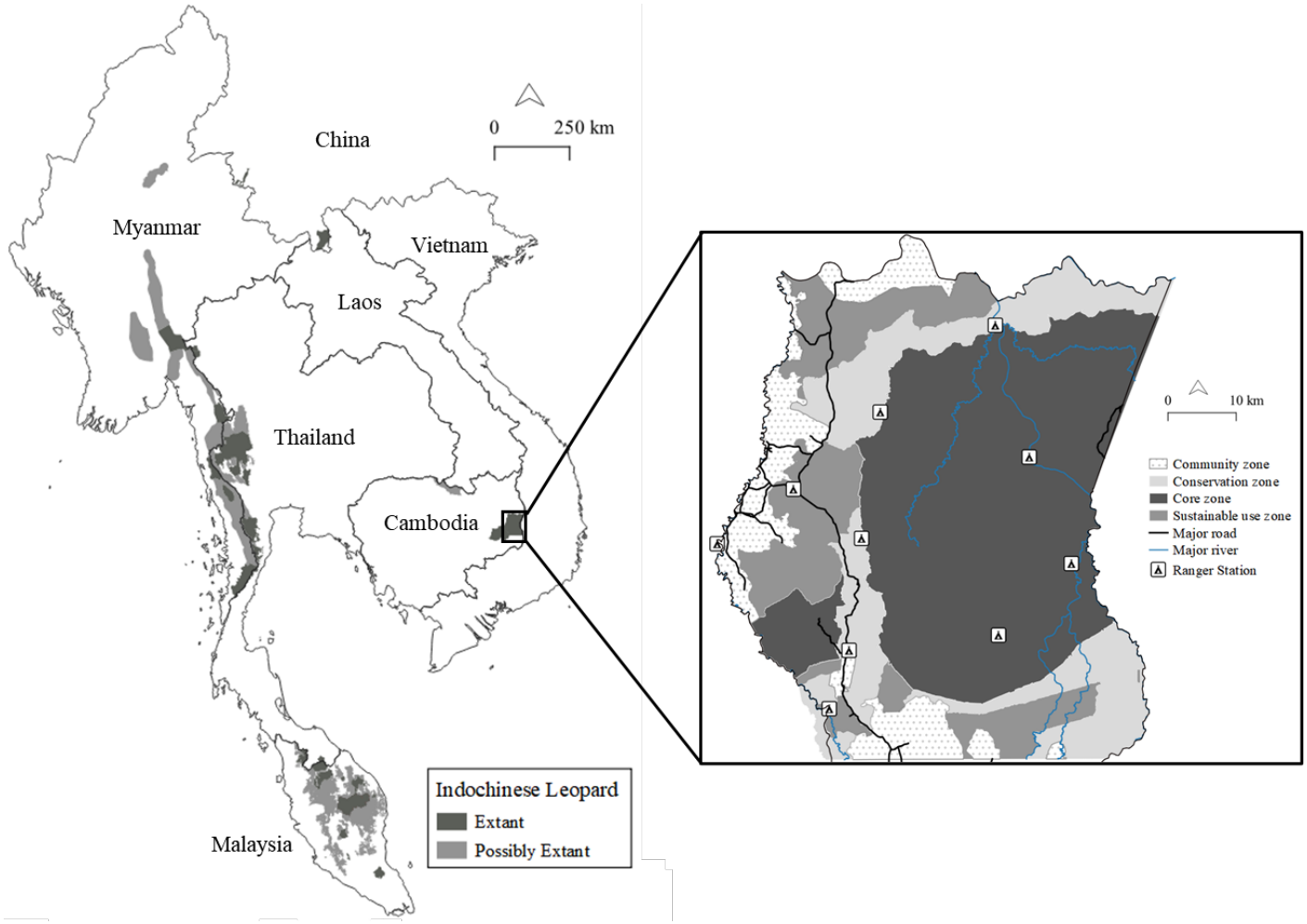


Figure 6.1 Current (extant and possibly extant) estimated distribution of the Indochinese Leopard (*Panthera pardus delacouri*) in Indochina, modified from Rostro-García *et al.* (2019). The insert shows the zonation of the study area, Srepok Wildlife Sanctuary, located in the Mondulkiri Province, Cambodia, and indicates the location of main ranger stations, major roads, and rivers.

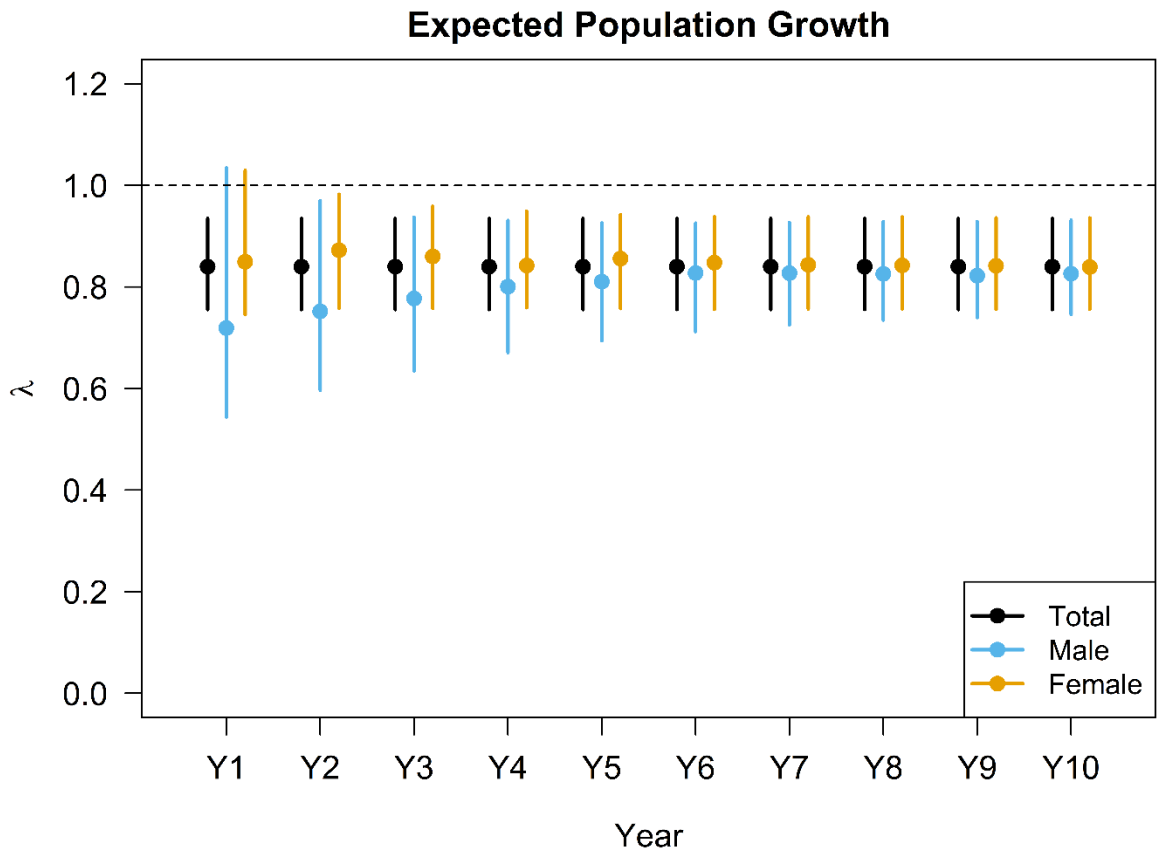


Figure 6.2 Total, female, and male Indochinese Leopard (*Panthera pardus delacouri*) expected population growth rate estimates between 2009 and 2019 for Srepok Wildlife Sanctuary, Cambodia, based on abundance estimates from an open population spatial capture-recapture model fitted to camera-trap data. The points and lines indicate point estimates and 95% highest posterior density intervals, respectively. The dotted line indicates a stable population size through time (λ = 1).

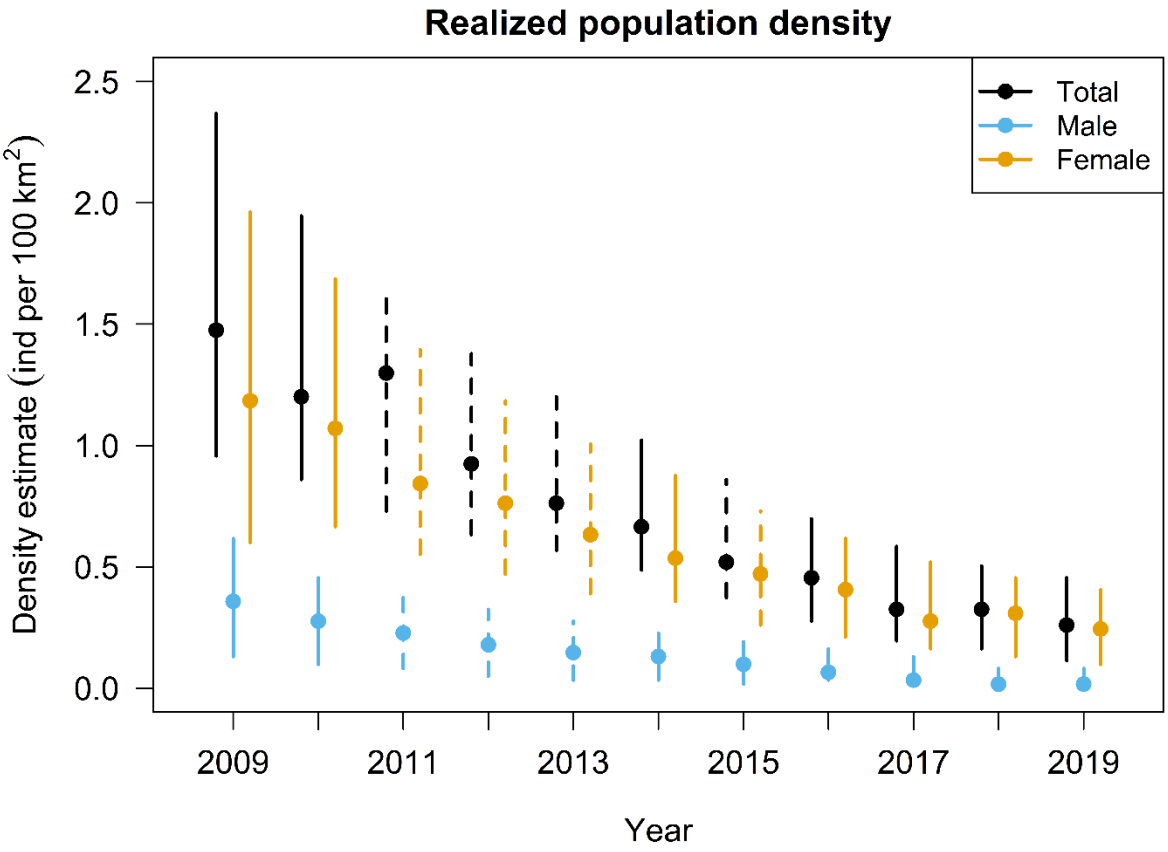


Figure 6.3 Total, female, and male realized population density estimates from open population spatial capture-recapture model fitted to camera-trap data of Indochinese Leopard (*Panthera pardus delacouri*) in Srepok Wildlife Sanctuary, Cambodia, between 2009 and 2019. The points and lines indicate point estimates and 95% highest posterior density intervals, respectively. Solid lines designate years with data collection, whereas dotted lines indicate years without data collection.

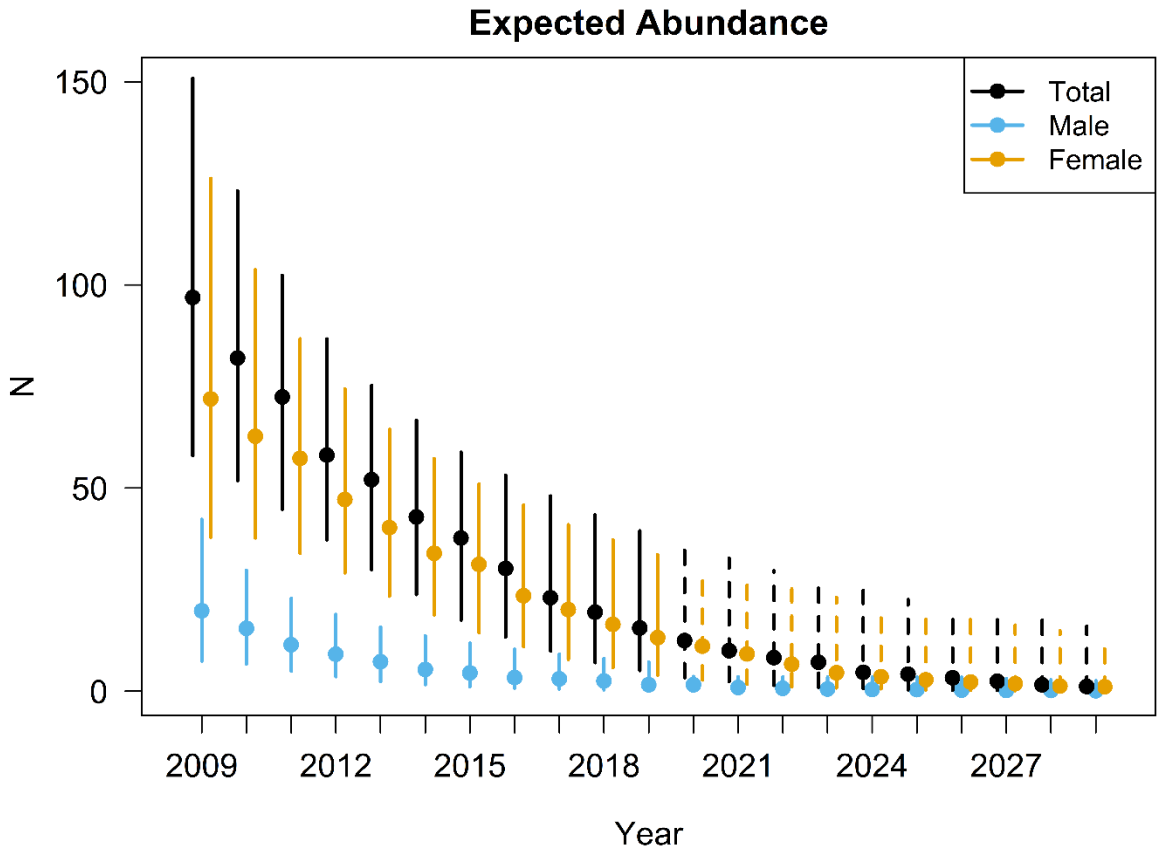


Figure 6.4 Total, female, and male Indochinese Leopard (*Panthera pardus delacouri*) expected abundance estimates between 2009 and 2019 and projected from 2020 to 2029 for Srepok Wildlife Sanctuary, Cambodia, derived from an open population spatial capture-recapture model fitted to camera-trap data. The points and lines indicate point estimates/projections and 95% highest posterior density intervals, respectively. Solid lines designate years corresponding to the study period, whereas dotted lines indicate years with projections beyond the study period.

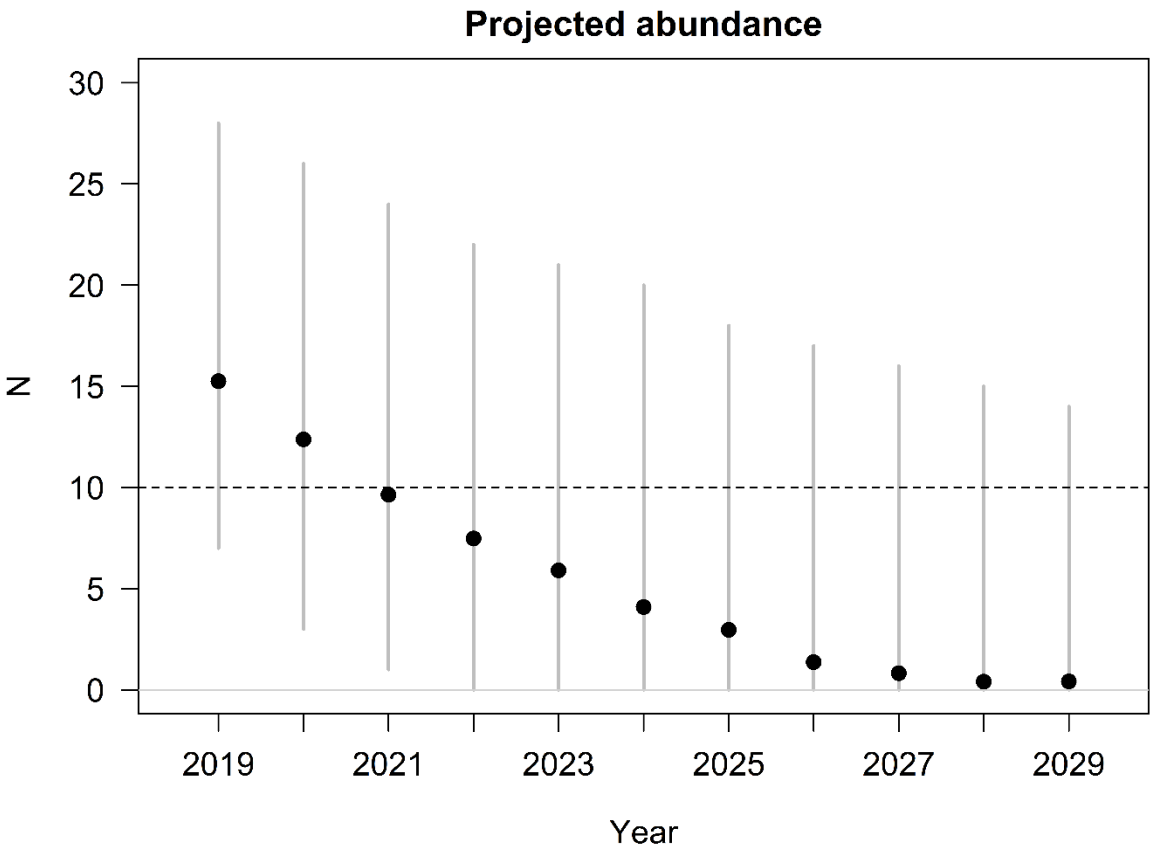


Figure 6.5 Indochinese Leopard (*Panthera pardus delacouri*) population projected 10 years into the future for Srepok Wildlife Sanctuary, Cambodia. The projection was accomplished through posterior sampling from an open population spatial capture-recapture model fitted to camera-trap data, and conditional on the realized abundance of the final year of data collection (2019). The black points and grey lines indicate point estimates and 95% highest posterior density intervals, respectively. The dotted line indicates the critical threshold for quasi-extinction, defined as the probability that the population size fell below 10 individuals.

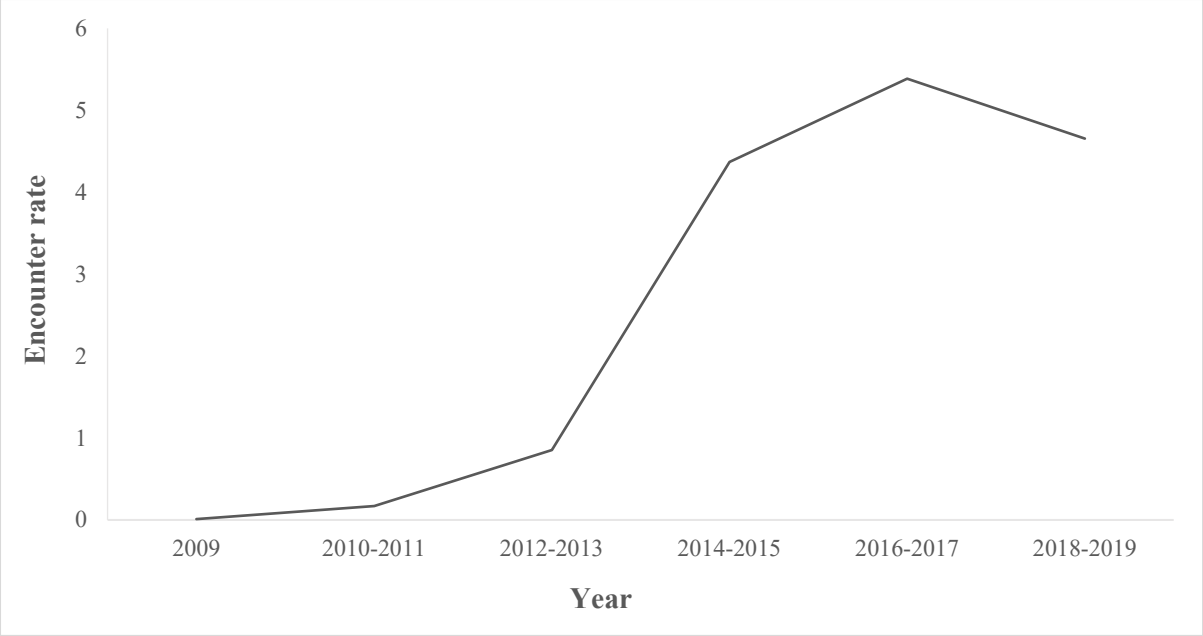


Figure 6.6 Lethal trap encounter rate, calculated as the number of lethal traps (e.g., snares and metal snap traps) encountered and removed per 100 km patrolled, derived from data obtained from the Spatial Monitoring And Reporting Tool (SMART) reported by rangers between 2009 and 2019 in Srepok Wildlife Sanctuary, Cambodia.

6.7 Supplementary Material

Appendix 6.1

Figure A6.1 Pairwise correlation between estimates of the pooled-sex activity centre relocation spatial scale parameter (σ^T) and: (a) survival (Φ), (b) female-specific recruitment (γ^f), and (c) male-specific recruitment (γ^m) obtained from an open population spatial capture-recapture model fitted to camera-trap data of Indochinese Leopard (*Panthera pardus delacouri*) from Srepok Wildlife Sanctuary, Cambodia, between 2009 and 2019.

Figure A6.2 Lethal trap encounter rate, calculated as the number of lethal traps (e.g., snares and metal snap traps) encountered and removed per 100 km patrolled, derived from data obtained from the Spatial Monitoring And Reporting Tool (SMART) reported by rangers between 2009 and 2019 in Phnom Prich Wildlife Sanctuary, Cambodia.

Table A6.1 Summary of Indochinese Leopard (*Panthera pardus delacouri*) camera-trap surveys conducted from 2016 to 2019 in Phnom Prich Wildlife Sanctuary, Cambodia. Trap nights represent the total number of days across all functional (at least 1 operating camera of a pair) camera-trap stations. F = female, M = male.

Table A6.2 Enforcement efforts deployed over 11 years (2009-2019) in Phnom Prich Wildlife Sanctuary, Cambodia. Data on distance patrolled and absolute number of lethal traps (e.g., snares and metal snap traps) were obtained from the Spatial Monitoring And Reporting Tool (SMART) and reported by rangers. The encounter rate was calculated as the number of lethal traps encountered per 100 km patrolled.

Table A6.3 Detection frequencies (number of independent events divided by total camera-trap days multiplied by 100) of mammals >2 kg and human-related events recorded in camera-trap surveys conducted in 2009 and 2019 in Srepok Wildlife Sanctuary, Cambodia.

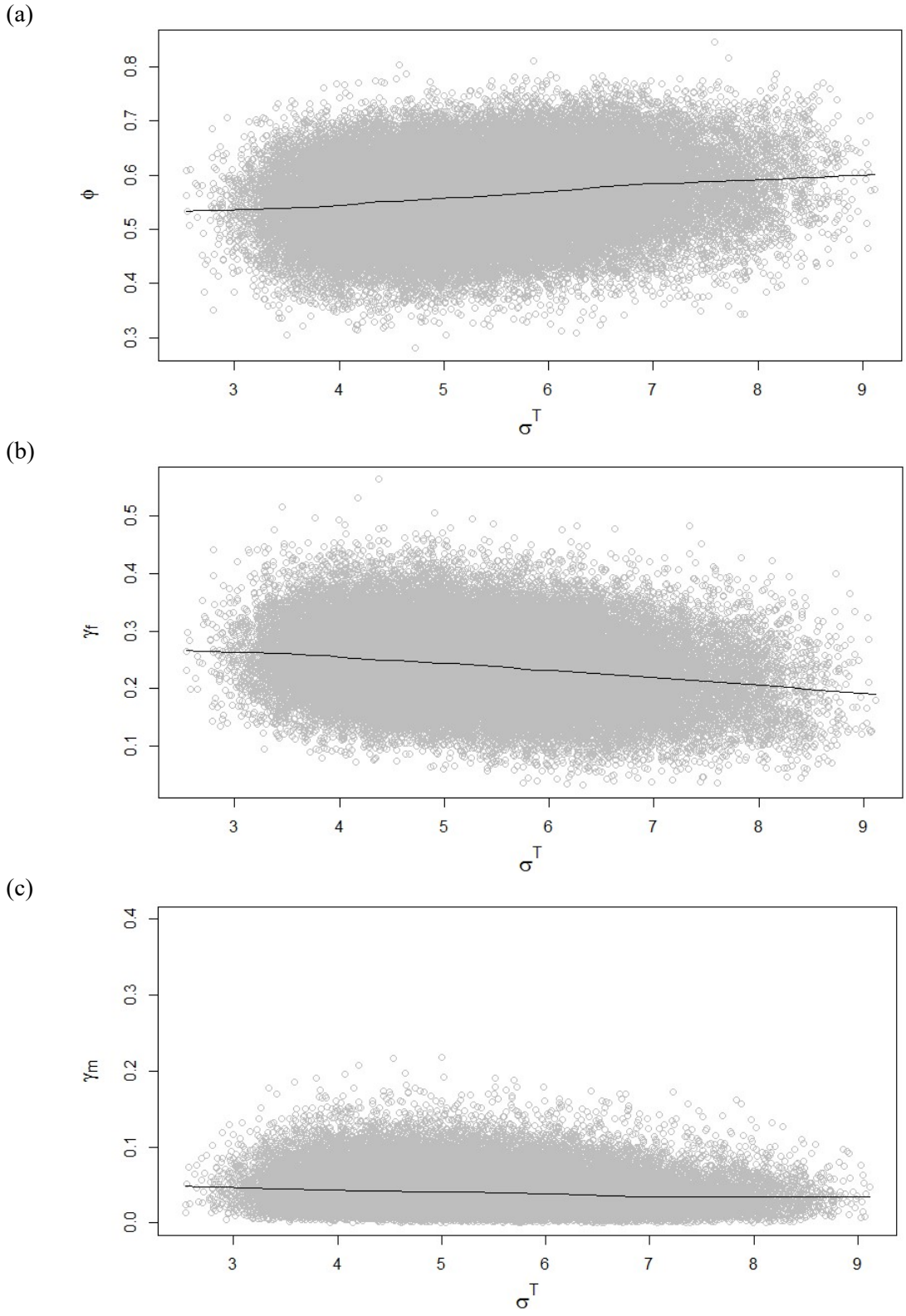


Figure A6.1 Pairwise correlation between estimates of the pooled-sex activity centre relocation spatial scale parameter (σ^T) and: (a) survival (Φ), (b) female-specific recruitment (γ^f), and (c) male-specific recruitment (γ^m) obtained from an open population spatial capture-recapture model fitted to camera-

trap data of Indochinese Leopard (*Panthera pardus delacouri*) from Srepok Wildlife Sanctuary, Cambodia, between 2009 and 2019.

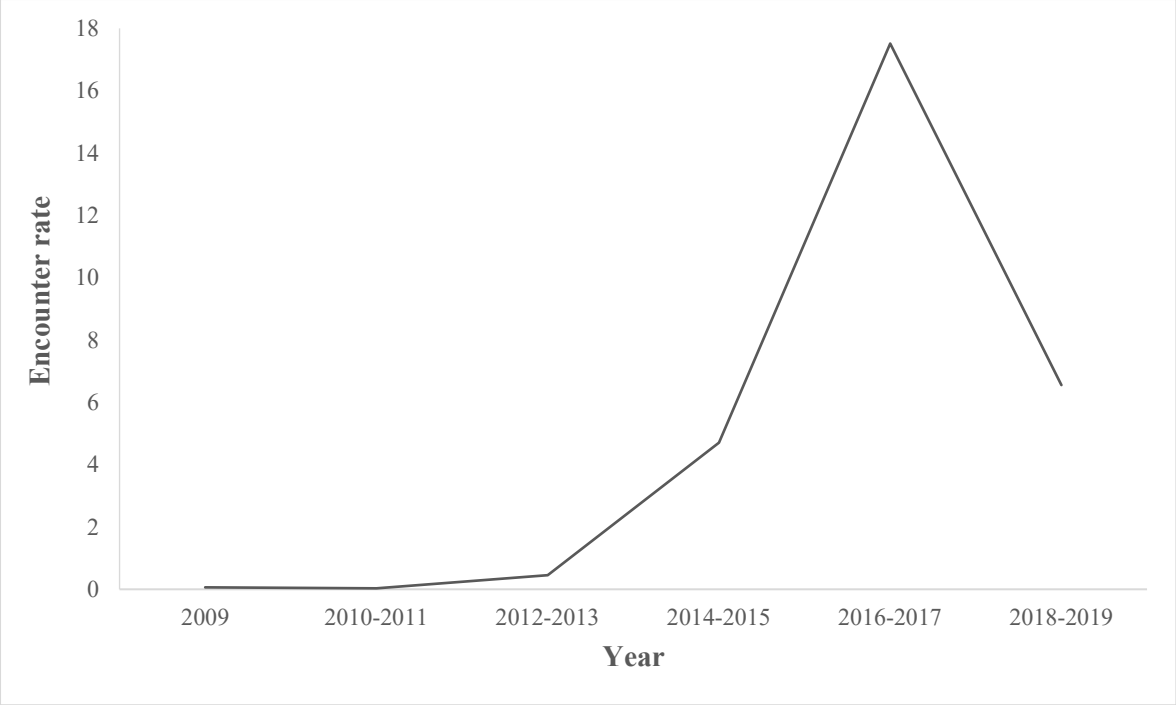


Figure A6.2 Lethal trap encounter rate, calculated as the number of lethal traps (e.g., snares and metal snap traps) encountered and removed per 100 km patrolled, derived from data obtained from the Spatial Monitoring And Reporting Tool (SMART) reported by rangers between 2009 and 2019 in Phnom Prich Wildlife Sanctuary, Cambodia.

Table A6.1 Summary of Indochinese Leopard (*Panthera pardus delacouri*) camera-trap surveys conducted from 2016 to 2019 in Phnom Prich Wildlife Sanctuary, Cambodia. Trap nights represent the total number of days across all functional (at least 1 operating camera of a pair) camera-trap stations. F = female, M = male.

Year	Trap nights	No. camera-trap stations	Stations detected	Total no. detections	Mean number of detections (range)	Individuals captured (F, M)	Cumulative no. individuals detected
2016	1,850	37	10 (27.0%)	29	5.8 (3-10)	5 (5, 0)	5
2018	3,231	42	11 (26.2%)	32	8.0 (5-14)	4 (3, 1)	7
2019	3,226	41	4 (9.8%)	10	5.0 (1-9)	2 (1, 1)	7

Table A6.2 Enforcement efforts deployed over 11 years (2009-2019) in Phnom Prich Wildlife Sanctuary, Cambodia. Data on distance patrolled and absolute number of lethal traps (e.g., snares and metal snap traps) were obtained from the Spatial Monitoring And Reporting Tool (SMART) and reported by rangers. The encounter rate was calculated as the number of lethal traps encountered per 100 km patrolled.

Year[a]	Number of Rangers[b]	Distance patrolled (km)	Number of lethal traps	Encounter rate
2009	39	8,189	5	0.06
2010	33	15,480	7	0.05
2011	31	19,551	4	0.02
2012	25	16,161	4	0.02
2013	38	9,946	115	1.16
2014	19	8,078	145	1.79
2015	41	12,398	818	6.60
2016	42	13,083	2,678	20.47
2017	20	11,527	1,632	14.16
2018[c]	21	3,237	754	23.29
2019	43	29,359	1,382	4.71

[a] information, available from monthly reports, considers yearly data 10 Dec-10 Dec instead of calendar years

[b] includes Ministry of Environment rangers, police rangers, army rangers, and community rangers. Recruitment of community rangers started in 2018.

[c] temporary absence of SMART reporting.

Table A6.3 Detection frequencies (number of independent events divided by total camera-trap days multiplied by 100) of mammals >2 kg and human-related events recorded in camera-trap surveys conducted in 2009 and 2019 in Srepok Wildlife Sanctuary, Cambodia.

Species – IUCN classification[a]	2009	2019
Bovidae		
Banteng (*Bos javanicus*) - EN[b]	3.72	1.11
Gaur (*Bos gaurus*) - VU[b]	0.92	0.25
Canidae		
Dhole (*Cuon alpinus*) - EN[b]	0.62	0.02
Golden Jackal (*Canis aureus*) - LC	0.12	0.20
Cercopithecidae		
Common Long-tailed Macaque (*Macaca fascicularis*) - VU	0.30	0.93
Southern Pig-tailed Macaque (*Macaca nemestrina*) - VU[b]	0.21	0.09
Cervidae		
Northern Red Muntjac (*Muntiacus vaginalis*) - LC	10.56	10.50
Sambar (*Rusa unicolor*) - VU[b]	0.12	0.07
Elephantidae		
Asian Elephant (*Elephas maximus*) - EN	0.86	0.89
Felidae		
Indochinese Leopard (*Panthera pardus delacouri*) - CR[b]	6.19	0.57
Jungle Cat (*Felis chaus*) - LC[b]	0.09	0.07
Leopard Cat (*Prionailurus bengalensis*) - LC	0.30	0.30
Herpestidae		
Crab-eating Mongoose (*Herpestes urva*) - LC	0.06	0.07
Hystricidae		
Malayan Porcupine (*Hystrix brachyura*) - LC	1.46	6.22
Leporidae		
Burmese Hare (*Lepus peguensis*) - LC	0.59	9.68
Mustelidae		
Greater Hog Badger (*Arctonyx collaris*) - VU[b]	0.18	---
Ferret Badger (*Melogale* spp.) - LC	0.12	0.18
Yellow-throated Marten (*Martes flavigula*) - LC	0.09	0.64
Suidae		
Wild Boar (*Sus scrofa*) - LC	7.47	19.47
Ursidae		
Sun Bear (*Helarctos malayanus*) - VU[b]	0.12	---
Viverridae		
Common Palm Civet (*Paradoxurus hermaphroditus*) - LC	1.07	1.00
Large Indian Civet (*Viverra zibetha*) - LC	0.89	4.07
Large-spotted Civet (*Viverra megaspila*) - EN	0.54	0.77
Small Indian civet (*Viverricula indica*) - LC	0.09	2.84
Human-related events[c]	6.07	124.42

[a] CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern.

[b] Species whose detection frequencies decreased during the study period.

[c] Human-related events = records of illegal anthropogenic activities (e.g., logging, poaching), as well as records of domestic animals (i.e., dogs and cattle) which were associated with humans.

CHAPTER 7

General Discussion

7.1 Meeting the Aims

The present study was conducted to gather information on the current status of the Leopard in Southeast Asia, an extremely biodiversity rich but highly threatened region (Hughes, 2017b). The study was motivated mainly by the lack of knowledge of the species in the wider region, which in turn posed a limitation to the management and conservation of its populations. The primary purpose of the study was to collect ecological information with an applied, conservation-oriented intent. Specifically, this thesis had two overarching aims: 1) to characterise and quantify Indochinese and Javan Leopard populations in areas within their current distribution in Southeast Asia, and 2) to identify the ecological parameters that determine Leopard presence in key populations of the region. For these aims, I first outlined the current distribution of the Indochinese Leopard and identified priority sites for its conservation. This was followed by the estimation of population parameters, notably density, for a baseline status assessment within key sites for Leopard conservation in the region, as well as investigations on other aspects of Leopard ecology, such as diet, habitat use, and temporal behaviour. The second purpose of the study was analytical-practical, aiming to examine current practices, and apply novel approaches to study the Leopard. All data Chapters, with the exception of Chapter 2, incorporated analytical strategies to handle the sparse data sets typical of the species in the region (see section 7.2.3). In addition, Chapter 4 was envisioned to provide information for future studies of the species in Southeast Asia, by proposing guidelines for conducting camera-trap surveys of Leopard and other similar-size carnivores persisting in low-density populations.

7.2 Key findings and contributions

7.2.1 ***Conservation-oriented contributions***

Indochinese Leopard status assessment

Chapter 2 represents the first in-depth assessment of the Indochinese Leopard, and showed that the subspecies now likely occurs in about 2-6% of its historical range. The study found that the Leopard is now 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. Consequently, three priority sites for the conservation of the subspecies were identified: a small, isolated population in eastern Cambodia, and the two remaining strongholds, Peninsular Malaysia, and the Northern Tenasserim Forest Complex (NTFC) along the Thailand-Myanmar border. This study underlined that the increased poaching for the illegal wildlife trade, especially wildmeat, likely was the main factor causing the decline of the Indochinese Leopard, with other potential contributing factors including habitat destruction, prey declines, and possibly disease. The results from this study led to a separate IUCN assessment of the Indochinese Leopard in 2019, in which the subspecies was classified as Critically Endangered (Appendix A).

Leopard status within key populations in Southeast Asia

By conducting the largest camera-trap study for Leopard in Southeast Asia, encompassing 7 sites across 4 countries, this study helped elucidate the conservation status of the Leopard and estimated densities, activity patterns, and habitat use of the species within key populations across the region. The findings of Chapter 3 showed that Leopard densities in several of the remaining populations within Southeast Asia were some of the lowest ever reported for the species, with levels of illegal human activities appearing to affect densities, habitat use and activity patterns of Leopard. The results indicated that the effects of humans differed between study areas located in the northern (Cambodia, Thailand) and southern (Malaysia, Indonesia) countries, likely due to differences pertaining to poaching, which itself likely was influenced by religious beliefs, socio-economic status, and geographical location. Importantly, the findings suggest that the overall prognosis of the species in the region is becoming increasingly bleak, and therefore the implementation of timely, effective, and area-specific strategies is required for the long-term conservation of Leopard in Southeast Asia.

Using reliable and repeatable techniques, this study provided baseline data, thereby facilitating the monitoring and future assessment of the species status in the study areas.

Ecology and population decline of the Indochinese Leopard in a priority site

In Chapter 5 and Chapter 6, the ecology and status of the Indochinese Leopard was studied in eastern Cambodia, in one of the last remaining viable populations in Southeast Asia. By using DNA confirmed scats, this study corroborated the adaptability of the species, which consumed 13 prey species, including the Banteng (*Bos javanicus*; 600-800 kg), making this the only known Leopard population whose main prey had adult weight >500 kg. This study was the first to determine the predation impact of Leopard in Asia, and showed in the study area the species only had a relatively small predation impact on ungulate populations. In addition, this study was the first to examine inter-sexual differences in diet and prey selection of Leopard in Asia, and revealed important distinctions between sexes: female Leopard filled a typical Leopard niche as predator of relatively small-sized ungulates, whereas male Leopard appeared to have expanded its dietary niche to include regular predation on Banteng, one the largest ungulate species. By using a novel approach, this study regrettably showed that the Leopard population in this priority site is under imminent risk of extirpation.

7.2.2 ***Practical contributions***

Camera trapping, often regarded as one of the most robust and effective non-invasive techniques to study wildlife populations (Green *et al.*, 2020), proved to be an efficient method to study these rare and cryptic subspecies of Leopard. This study also corroborated that individual identification of melanistic Leopard is possible using camera traps with infrared light (Hedges *et al.*, 2015), thereby allowing for the first reliable density estimates of several additional melanistic Leopard populations (Chapter 3). This technique can be especially useful in Southeast Asia, where the majority of the remaining Leopard populations (both Indochinese and Javan) have melanistic individuals. This is a more reliable technique for identifying individuals of this phenotype compared to other techniques used in the past (e.g., individual identification based on body size and shape, or scars). Camera-trap

data also provided auxiliary information that help better elucidate other aspects of Leopard ecology (e.g., temporal, and spatial partitioning with humans and prey). Because camera traps were operating simultaneously, large amounts of effort were rapidly accumulated, which increased their suitability to study the characteristically low-density populations of Leopard, while also facilitating data collection on other non-target species for which information on their ecology and conservation status could be obtained (e.g., see Appendix B, Appendix C, and Appendix E). Furthermore, the extraction of human-related events derived from camera-trap data aided in the understanding of the anthropogenic pressures impacting the different study areas (e.g., frequency, type). Because SMART and similar enforcement data often are subject to bias (Ibbett *et al.*, 2020b, Keane *et al.*, 2011) and influenced by a wide array of factors (e.g., patrolling strategy, coverage, skills, imperfect detection of snares), this study showed that incorporating camera-trap data also can be advantageous to provide further information on illegal human activities and potential impacts, which is particularly useful in areas where anthropogenic pressures are prevalent but a causal effect is difficult to determine.

In addition, in Chapter 4 the performance of SCR models in low-density populations surveyed with camera traps was investigated by using simulated and empirical data under a range of ecologically realistic population scenarios and commonly used survey designs. The findings suggested that some camera-trap studies targeting low-density populations may not be meeting the requirements necessary to produce unbiased population parameter estimates, likely resulting in overestimates of densities which ultimately can be counterproductive for the conservation of the target species. Consequently, this study provided specific recommendations for future camera-trap studies to facilitate the applicability of SCR methods when studying low-density carnivore populations.

7.2.3 ***Analytical approaches***

This study made extensive use of hierarchical models for data analysis, which due to their flexibility and ability to account for ecological and observational processes alike, provided both conceptual and practical advantages (Royle and Dorazio, 2008). Conceptually, the use of hierarchical models allowed for a better understanding of the system and the different components at play. Practically,

the use of these models permitted to draw stronger inferences about the Leopard by allowing to share information among the sparse data sets obtained, while accounting for sources of variation that arise from the different components (Royle *et al.*, 2014). In addition, these models allowed for the combination of data collected at different scales (e.g., primary and secondary periods of the camera-trap surveys) and across different surveys within a modelling framework, demonstrating this strategy can be an avenue to improve parameter estimates of the small-sample sizes that characterise data sets of the species in the region. These models were analysed in a Bayesian framework, where the posterior distributions of all unknown quantities, including latent variables, were characterised with Markov Chain Monte Carlo (MCMC) simulation methods, allowing for the exploration of several relevant aspects of Leopard ecology (Royle and Dorazio, 2008). In addition, the use of hierarchical Bayesian open population spatial capture-recapture (open SCR) models facilitated the estimation of population demographic parameters, including during years when surveys were not conducted. Although further refinements are required, this study showed that open SCR models represent a favourable and flexible framework for assessing and monitoring wildlife populations. By explicitly incorporating information on the movement and spatial location of an individual into the model, open SCR models offered a more realistic representation of the ecological and detection processes and allowed for an efficient utilization of the available data (Gardner *et al.*, 2018, Royle *et al.*, 2014, Satter *et al.*, 2019). This represents the first study to use open SCR models on a Leopard population, which in turn allowed for the first-ever study on long-term population dynamics of the species in Asia (Chapter 6).

7.3 Study limitations and recommendations to improve research on Leopard

7.3.1 ***Data gathering and study design***

Although this thesis shed light on the status of the Indochinese Leopard, the lack of recent empirical knowledge derived from systematic surveys hampered a robust, quantitative status assessment of the subspecies in certain areas (e.g., Kayin state in Myanmar, forest reserves of Peninsular Malaysia). This in turn, could have resulted in under- or over-estimates in numbers and distribution of the

subspecies within extant and possibly extant areas (Chapter 2). In order to more accurately elucidate the current status of the Indochinese Leopard in Southeast Asia, future studies should aim to conduct research in areas where the status of the subspecies is virtually unknown (due to a complete lack of surveys or lack of abundance data), including several protected and unprotected areas within the NTFC along the Thailand-Myanmar border, Krau Wildlife Sanctuary and forest reserves in Peninsular Malaysia, and Kayin state in Myanmar.

The camera-trap survey design (e.g., camera placement, sensitivity settings) used throughout this study targeted the Leopard and other relatively large (>1 kg) ground-dwelling species; thus, reducing the detection probability of several smaller species or those with arboreal or semi-arboreal habits, some of which were considered potential prey species of the Leopard (e.g., macaques). Moreover, area-specific differences (e.g., habitat structure) likely resulted in variation of detection probability of some of the species considered as potential prey. Although the levels of heterogeneity in detection probability and its implications for estimates of Leopard habitat use were somewhat diminished when grouping potential prey and incorporating an area level random effect, future studies should investigate in more detail species-specific influences of prey on Leopard habitat use. In addition, while findings from this study suggest there are differences between the study sites located in the northern and southern countries, poaching drivers often are the result of complex and locally-specific processes not investigated in detail here; thus, further research is required to obtain a more holistic understanding of the reasons for poaching and its effects on wildlife communities.

Because several of the study areas became inaccessible during the wet season, the study was exclusively conducted during the respective dry seasons. Consequently, results were biased towards the latter season, in which habitat conditions may be harsh (e.g., extensive annual fires). However, results from the rainy season may have been different given that human activity presumably decreases owing to the growing inaccessibility, while prey numbers and distributions possibly changes, potentially altering Leopard temporal activity, movements, and feeding behaviour (Balme *et al.*, 2017b). Nevertheless, for a long-lived territorial species such as Leopard, dry season estimates should be representative of density more generally, as major changes in density between seasons

were not expected. Similarly, dry season estimates of habitat use should provide an adequate representation of the overall ecology of the species and its relationships with both humans and prey.

There was a difference in the success rate of identifying individual melanistic Leopard from photographs depending on the camera type used. Based on field photographs, and tests using captive melanistic Leopards as well as museum skins of melanistic felids, it became apparent that the passive IR feature in the Panthera V6 IR cameras often leads to inadequate exposure during daytime events, thereby hindering the visibility of uniquely identifiable spots. During night-time the Panthera V6 IR used an IR flash that successfully illuminated the spots on melanistic Leopards. However, 81% of photos of melanistic Leopard in Taman Negara National Park (TNNP) were from the daytime; thus, many were affected by the underexposure. In contrast, Reconyx HC500 cameras, used in Pasir Raja Selatan Forest Reserve (PR), successfully illuminated the spot patterns of melanistic Leopard in all photos, both day and night, similar to findings reported by a previous study (Hedges *et al.*, 2015). Adjustments were incorporated in subsequent field surveys to improve the exposure of daytime events taken by the Panthera V6 IR cameras, including moving the cameras closer to the trails, because illumination of spot patterns increased with closer proximity of the Leopard to the camera. Although 27% of the photos from TNNP had to be discarded due to lack of individual identification, this percentage was similar to several previous studies of large felids where 21-50% of the photos had to be rejected due to poor quality and lack of individual identification (Alexander *et al.*, 2015, Gray and Prum, 2012, Steinmetz *et al.*, 2009). Nonetheless, because discarding photos is particularly undesirable under the data-sparse circumstances typical of Leopard in the region, future research on remaining Leopard populations of Southeast Asia, all of which contain melanistic individuals, should consider incorporating adjustments that increase individual identification success rate. Recent advances (e.g., spatial partial identity models) that use the spatial location where partial identity samples (i.e., individuals whose identity is only known from a single flank) are captured to probabilistically resolve their complete identities should be considered when appropriate, in order to allow for single-flank photos to be used in the analysis and consequently improve inferences (Augustine *et al.*, 2018).

*7.3.2 **Analytical considerations***

It was evident from this study that obtaining sufficient data to estimate Leopard population parameters accurately is a challenging endeavour, particularly in defaunated areas. In addition, camera-trap surveys of large carnivores such as Leopard are resource and time intensive, and despite the efforts, logistical (e.g., area accessibility, man-hours) and financial constraints, alongside area-specific challenges (e.g., high theft rate), precluded larger areas from being surveyed. This, in turn, likely affected the precision of the estimates, which could have been improved with additional sampling stations. To counter data sparsity, models that integrated the sparse data from the different study areas were used for the purpose of obtaining the best possible estimates. Particularly, I was motivated to use the sparse data because, despite the myriad of persistent threats causing the region-wide decline of these understudied, Critically Endangered subspecies, reliable SCR density estimates within the region were only available for 2 areas by the time the study commenced. Small sample sizes often hinder population parameter estimates of threatened, rare, and understudied species, which are most in need of status assessment and conservation action (Gardner *et al.*, 2010). Thus, while inferences that can be drawn based on the data might be weak for certain areas, they still provide baseline information that can serve as a more appropriate foundation for conservation planning than traditional guesstimates. Future studies should strive to use sampling and analytical strategies (e.g., increasing area covered and number of stations, combining data sources) that optimise the precision and reliability of the parameter estimates.

The sparsity of the data sets precluded the investigation of certain aspects relevant to fully assess the population status of the species. For instance, in Chapter 6 the temporal variation in demographic rates or possible Allee effects of the population of Srepok Wildlife Sanctuary could not be evaluated due to the sparse data. This in turn, likely resulted in overestimates of the population persistence probability by assuming constant survival and per capita recruitment, when in reality these likely declined through time. However, because the local extirpation of the population is nonetheless imminent, it seemed important to provide estimates as quantitative evidence of the species status in the landscape, and the implications that this population decline had for the overall conservation of the subspecies in the wider region.

In order to combine data from multiple surveys, only predictor variables (e.g., landcover) available for all study areas were used to explore Leopard habitat use. However, finer resolution layers may provide additional area-specific information not explored in this study. In addition, the model approach used to investigate Leopard habitat use was fundamentally explorative (i.e., covariate selection can be considered more hypothesis generating than testing). Although covariates known to affect the species elsewhere were used, such an approach can be seen as a form of 'fishing expedition', which Burnham and Anderson (2002, p. 147) refer to as "poor strategy". However, due to the insufficient knowledge of the species in the region, such an explorative scheme seemed the most appropriate to ensure that relevant region-specific factors were considered.

The simulations conducted to investigate the overall performance of SCR models when studying low-density populations using common study designs were general and based on a limited number of scenarios. Consequently, other survey designs may yield different results than those obtained in this study. For instance, the designs evaluated, both under uniform and multi-cluster layout, followed a regular spatial pattern (i.e., same spacing) of the stations. However, an irregular spatial structure (i.e., different spacing between stations) could have resulted in an enhanced resolution of the movement distances and thus in improved estimates of the spatial scale parameter σ (Dupont *et al.*, 2020). Similarly, the simulations were based on a fixed-square simulated study area that, although it maintained the spatial extent constant to mimic field conditions, may not be representative of problems encountered when surveying irregular areas in practice (e.g., remoteness precluding accessibility). In addition, other camera-trap configurations (e.g., 3x3 or 4x4 multi-cluster layouts), which could have provided better population parameter estimates (Clark, 2019), were not explored as the scenarios were limited to consider the number of stations frequently deployed in camera-trap studies of the region, in order to reflect the limitations likely to be encountered by local researchers (e.g., upper bound of available camera traps). Therefore, future research should consider design optimisation (Dupont *et al.*, 2020, Durbach *et al.*, 2021, Efford and Boulanger, 2019), adapted to study-specific considerations, including ecology of the target species, survey area characteristics, resource availability and logistical feasibility.

Further chapter-specific limitations were given in the respective sections of Chapters 3-6.

7.4 The plight of the 'common' Leopard

Till recently, the Leopard was assumed to warrant little conservation concern because it was considered, as its name implies, 'common' throughout most of its range. However, this study showed the species is far from common in Southeast Asia, where two endemic and Critically Endangered subspecies survive in small and isolated populations. These conditions could predispose the species to inbreeding depression and increases extinction risks from stochastic events. In a regional context, Leopard occurrence seems to be almost entirely restricted to protected areas, only with the exception of few forested areas in Java, Peninsular Malaysia, and the NTFC.

The inherently changing landscape and fast developing economies of Southeast Asia have rapidly altered the situation of the species in the region, and caused even recent (e.g., 5-10 years old) assessments, particularly of the Indochinese Leopard, to become obsolete. For example, the Indochinese Leopard assessment from Chapter 2 showed that by 2015 the subspecies still occurred in 7 different sites across Southeast Asia, but further results from this and other recent studies indicate the Leopard now is functionally extinct if not fully extirpated from 4 of those sites: Khlong Saeng-Khao Sok complex in Thailand, Htamanthi Wildlife Sanctuary and Rakhine Yoma Elephant Range Wildlife Sanctuary in Myanmar, and Eastern Plains Landscape (EPL) in Cambodia. Camera-trap surveys conducted in Htamanthi Wildlife Sanctuary, as well as surveys near and within the border of Rakhine Yoma Elephant Range Wildlife Sanctuary in Myanmar failed to detect the Leopard, despite the efforts from three different survey campaigns (Cremonesi *et al.*, 2021). This, together with the imminent extirpation of the species from the Eastern Plains Landscape of Cambodia (Chapter 6), and probable local extinction in the Khlong Saeng-Khao Sok complex (Chapter 3, Petersen *et al.*, 2020), provide further evidence that Leopard populations continue to drastically decline and even become extirpated in areas that harboured the species only 5 years ago. Consequently, the Indochinese Leopard now occurs only in two priority sites, which are considered the last strongholds of the subspecies: Peninsular Malaysia and the NTFC. Similarly, for the Javan Leopard only 3 national parks have been identified to potentially support populations of more than 50 individuals (i.e., Meru Betiri, Gunung Halimun Salak, and Ujung Kulon; Wibisono *et al.*, 2018).

Alarmingly, the conservation of the two subspecies cannot be assured even within their priority sites. For instance, the Javan Leopard priority sites occur within highly fragmented landscapes that are considerably isolated, making immigration from nearby populations unlikely and increasing sensitivity to within-population mortalities. Similarly, 80% of forest habitat in Peninsular Malaysia occurs within forest reserves rather than protected areas (Rayan and Linkie, 2015). Although the results of this study demonstrated the conservation value of forest reserves as supplements to protected areas (Chapter 3), these reserves offer little protection to wildlife as they are primarily designated for selective logging rather than wildlife conservation (Rayan and Linkie, 2016) or alternatives more amenable to biodiversity such as sustainable logging (Sollmann *et al.*, 2017). In fact, about three million hectares, equivalent to 61% of these forest reserves, are defined as Production Forests, and thus predominantly assigned for commercial selective logging (Rayan and Linkie, 2020). Recently, these reserves also have fallen under threat from clearance for monoculture plantations. For example, the total area of forest reserves designated for rubberwood plantations has expanded dramatically, leaping from 1,626 ha in 2006 to 120,000 ha in 2018, with a targeted expansion to 375,000 ha by 2020 (Abdul Aziz *et al.*, 2010, Rayan and Linkie, 2020). Although a new set of standards established in 2020 (i.e., Malaysian Criteria and Indicators for Sustainable Forest Management) prevents more than 5% of certified forests to be converted to plantations (MC&I SFM, 2020), poorly managed logged-over forests remain under threat of being classified as degraded forest and then converted to other land uses (Rayan and Linkie, 2020). The remaining forest blocks in Malaysia are under threat as they become increasingly fragmented by the infrastructure development (Clements *et al.*, 2014a) and the expansion of monoculture plantations (Abdul Aziz *et al.*, 2010, Clements *et al.*, 2010). Accordingly, from 2000 to 2012, Malaysia lost over 14% of its forest, a percentage of loss that exceeded that of any other country of the world during the same time period (Hansen *et al.*, 2013). Consequently, many forested areas in Malaysia, and the wildlife inhabiting them, might be at peril from these major habitat transformations (Aziz *et al.*, 2010, Clements *et al.*, 2010, Jain *et al.*, 2014, Shevade and Loboda, 2019).

Analogously, Leopard conservation cannot be assured within the NTFC, a complex that is not managed as a whole (i.e., no international cooperation in planning and management) and where the ongoing political reform and increasing levels of infrastructural projects threaten to alter this area, which represents the largest tract of intact forest landscape left in Southeast Asia. Amongst ongoing developmental projects the Dawei Special Economic Zone and its planned road link stand out for its potential to negatively affect wildlife conservation in the region (Helsingen *et al.*, 2015). For example, by cutting through the NTFC, the Dawei road will fragment this high-priority conservation landscape, which is a key site not only for the conservation of Leopard but of several other species (e.g., Tiger, Asian Elephant). These infrastructural projects, alongside commercial agriculture, expanding agroforestry areas, social change, and development, are likely to exacerbate threats, notably overexploitation of wildlife (Aung *et al.*, 2017, Clingen, 2019, Connette *et al.*, 2017). This is particularly true for previously remote areas of Myanmar, where, although a tenuous ceasefire has existed since 2012, political settlement to end armed conflict have not been reached yet, and where the ongoing political reform, increasing levels of foreign investment, de-mining and clearance of military encampments can facilitate extractive and exploitative economic development (Clingen, 2019, Moo *et al.*, 2017). Although the Thai side of the NTFC suffers from different pressures, it may also be unable to ensure Leopard conservation as the success of Thai protected areas in conserving biodiversity has been considered somewhat ambiguous (Singh *et al.*, 2021).

Regrettably, this study showed that even within protected areas of the remaining strongholds the status of the Leopard is mostly dire, with often low and decreasing populations. Although the severity of the decline in numbers and distribution cannot appropriately be quantified in all remaining Leopard populations of the region due to the lack of baseline data and recent surveys, evidence from well-monitored localities (e.g., EPL, TNNP-Kenyir Wildlife Corridor) suggest ongoing declines of the Leopard populations. There is no obvious indication to assume that these localities are not representative of the overall Leopard population trend in Southeast Asia and southeastern China. Instead, these likely represent a microcosm of what is transpiring across the wider region.

During the course of this study, it became apparent that the primary cause for the precipitous decline of the Leopard populations of Southeast Asia likely is the dramatic increase in anthropogenic

pressures, notably indiscriminate poaching. Southeast Asian countries have long been implicated in the illegal wildlife trade by functioning as sources, distributing hubs, transit routes, and destination wildlife markets (Jiao *et al.*, 2021). Aside from geographical proximity to both China and Vietnam, which are large consumers of wildlife products, several other factors have contributed to this reality, including endemic poverty, poorly resourced law enforcement, lax border security, corruption, and inadequate legislation (Jiao *et al.*, 2021). Currently, one of the major drivers of poaching, particularly in eastern Southeast Asian mainland, is the high demand for wildmeat, often regarded as a delicacy or a status symbol, by middle- and upper-class urban consumers (Drury, 2011, Sandalj *et al.*, 2016, Shairp *et al.*, 2016). Snares, the predominant form of poaching in Southeast Asia, represent an insidious and persistent threat to wildlife, causing defaunation and a conservation crisis across the region, including in designated protected areas (Gray *et al.*, 2018). Frequently set in large numbers by commercial poachers, snares can capture species either intentionally or as a bycatch, thus, representing a direct threat to most wildlife, including the Leopard (Belecky and Gray, 2020, Gray *et al.*, 2018). Although the Leopard is legally protected in China and all Southeast Asian countries, and included in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS), current enforcement of national laws is insufficient to provide effective protection to the species throughout most of its remaining range. Accordingly, the Leopard, which is both consumed as wildmeat and used in Traditional Chinese Medicine, was 1 of the 13 most common species offered in wildlife restaurants in Vietnam (Anh and Wyatt, 2013), and the most frequently recorded species in an investigation of big cat trade in Myanmar and Thailand, with a minimum of 167 individuals recorded in trade in a period of less than 10 years (Oswell, 2010).

While poaching in the Sundaic sites (i.e., Peninsular Malaysia and Java) is presumably not as extensive as in eastern mainland Southeast Asia, the wildlife there is not exempt from this threat. For example, foreign intruders undertaking illegal activities (e.g., snaring) have become increasingly prevalent in Peninsular Malaysia over the past 5-10 years (Belecky and Gray, 2020, Ten *et al.*, 2021), representing a threat to wildlife inhabiting protected and unprotected forests alike. In addition, seizure records from 24 incidents reported during an 8-year period in Indonesia amounted to about

51 Javan Leopards, a subspecies which alongside overexploitation for the illegal wildlife trade also suffers from retaliatory killings (Gomez and Shepherd, 2021). Alarmingly, even mountainous and inaccessible pockets of forest, such as the Aceh Province in northern Sumatra, Indonesia, are experiencing snaring, with at least 843 snares documented by anti-poaching teams in 2018 (Figel *et al.*, 2021).

Despite being the major driver of defaunation in the region, currently there are important gaps in wildlife protection legislation in relation to snaring. For instance, of the 8 large biodiverse countries in the Association of Southeast Asian Nations (ASEAN) region, only 1 (Malaysia) legally defines snares, and only 2 (Malaysia and Thailand) explicitly prohibit already assembled snares within protected areas (Belecky and Gray, 2020). Worryingly, no country to date prohibits the possession of materials that can be made into snares within protected areas (Belecky and Gray, 2020). Overall, pressures on the wildlife of the region have increased and are expected to continue given the ever-increasing demand for wildlife products and the consequent expansion of the empty-forest syndrome throughout the region. In the absence of scaled-up enforcement and major societal changes that curb the demand, poaching likely will continue to expand as areas become increasingly devoid of wildlife, forcing the movement of illegal activities into more remote areas. Consequently, this displacement of illegal activities is expected to affect areas currently less exposed to anthropogenic pressures, such as TNNP, to maintain comparable levels of offtake. This in turn will have consequences beyond wildlife by affecting the nutritional security of indigenous people and local communities that depend closely on natural resources for their health and wellbeing (Belecky and Gray, 2020).

The thriving illegal wildlife trade, together with insufficient law enforcement within parks, rapidly increasing infrastructure development, and high human densities, have contributed to unsustainable levels of indiscriminate poaching throughout most of Southeast Asia. As the rarity of Leopard and Tiger increases, the prices of big cat products paid by consumers likely will increase substantially, which incentivise harvest and increase the already elevated pressures from the wildmeat trade (Holden and McDonald-Madden, 2017). This change in market dynamics can drive small populations to the brink of extinction, a phenomenon often referred to as “anthropogenic Allee

effect" (Courchamp *et al.*, 2006, Holden and McDonald-Madden, 2017). These factors have synergistically pushed Leopard conservation, already suffering from large shortfalls, into a triage. The status of the species in the region is critical, with recovery efforts being difficult at best. In order to change the bleak prognosis, a plethora of multi-faceted interventions is required, including an urgent shift in the current paradigm.

7.5 Conserving the Leopard in Southeast Asia

7.5.1 Shifting the paradigm and other short-term strategies

Currently, conservation efforts in the region, mostly targeted for Tiger, focus on individual sites, and do not account for larger landscape dynamics. However, it is crucial that conservation efforts shift towards a landscape-scale approach (Goswami and Vasudev, 2017, Vasudev *et al.*, 2021), that strives for a single range-wide strategy for the conservation of Leopard and other wildlife, with interagency collaboration in conservation, research, and management, as opposed to the insular and site-specific approaches typically taken thus far. With only 2 remaining strongholds for the Indochinese Leopard, and presumably 3 for the Javan Leopard, it is imperative that these sites become better protected to ensure the long-term viability of the species in the region. To maximise the effectiveness of interventions and make optimal use of current limited conservation resources, initial efforts should focus on safeguarding the species in protected areas within the strongholds that harbour viable populations. Other short-term strategies include increasing and improving efforts that reduce anthropogenic stressors within and around protected areas, with particular attention given to the pervasive snaring (see section 7.5.3). In addition, the importance that well-managed forest reserves can have for Leopard and other wildlife conservation needs to be highlighted to governments and other stakeholders so that protection in these areas is increased. For instance, the TNNP, the largest protected area of the country and a conservation priority landscape within Peninsular Malaysia, represents the only large forested land gazetted for perpetuity that is under direct jurisdiction of the Department of Wildlife and National Parks, and thus the Federal Government (Kawanishi and Sunquist, 2004). Therefore, by expanding protection to surrounding forest reserves, the greater

Taman Negara Landscape (i.e., TNNP and surrounding forest reserves) likely could offer the best chance for long-term viability of the Leopard population inhabiting this stronghold. In addition, through the maintenance and improvement of habitat linkages the greater Taman Negara Landscape could increase chances of dispersal between Leopard populations of the Peninsula, including with the other 2 priority landscapes (de la Torre *et al.*, 2019, Kangayatkarasu *et al.*, 2016, Regional Planning Division, 2009a, Regional Planning Division, 2009b), thus potentially playing a major role as a regional and global hotspot for Leopard and several other Threatened species, including the Tiger.

7.5.2 Connectivity

The connectivity of remaining populations, not only those within protected areas, which are cornerstones for Leopard conservation in the region, but also with other areas (e.g., forest reserves), will be necessary to ameliorate the risks of small population size and isolation, and ensure the long-term viability of remaining populations of the region. Recognizing that several of the protected areas do not hold viable populations and that other areas that could be ordained as additional wildlife reserves are becoming increasingly limited (West *et al.*, 2008), this shift needs to occur promptly and through international collaboration. The interconnection of the subpopulations (i.e., metapopulation) would reduce the risks associated with demographic, genetic and environmental stochasticity by increasing the overall population size, allowing for the supplementation of individuals and the recolonization in areas where the species has been locally extirpated (Hanski, 1998, Hanski and Ovaskainen, 2000). This is particularly important in Asian Leopard populations which are characterised by higher population structuring, stronger isolation, and lower heterozygosity than African Leopard populations (Paijmans *et al.*, 2021). Because most of the region is characterised by fragmented landscapes where humans are omnipresent, it is important that the degree of isolation among populations is assessed and that possible dispersal and movement barriers are identified.

By structurally connecting otherwise non-contiguous patches, corridors can act as instruments to achieve landscape linkages and population connectivity (Chetkiewicz *et al.*, 2006). Although there is little knowledge of the species outside protected areas, forested reserves, and some

plantations, which often coincide with less intensively used areas by humans, may aid in the development, improvement, or expansion of such corridors, particularly in Peninsular Malaysia and the NTFC. Careful planning and execution are required to maximise the conservation potential and ensure the implementation of ecologically functional corridors (Jain *et al.*, 2014). For that, sufficient resources need to be allocated, and financial and legal frameworks need to be clearly defined to prevent forest conversion and biodiversity losses by protecting corridors from development projects (Jain *et al.*, 2014). Importantly, evaluations based on empirical data that assess the potential risks (e.g., wildlife disease transmission, colonization of invasive species) and negative effects (e.g., sink habitat patches, human-wildlife conflict) of connecting populations are necessary to ensure that mitigation plans and alternatives are delineated in corridor design and implementation. Consequently, the occurrence of Leopard in potential areas needs to be investigated to identify existing populations outside protected areas, understand the characteristic that favour the occurrence of the species, and evaluate the likelihood of Leopard survival given the socio-cultural landscape. Policy statements, agreed upon by different government entities (e.g., legislation agreements at ministerial and municipal level) likely represent a powerful tool for implementing such conservation efforts (Zeller *et al.*, 2013). In addition, a landscape framework that focuses on iconic species (e.g., Asia's big 5: Tiger, Leopard, Elephant, Gaur, and Banteng) and that could potentially provide economic revenue from tourism, likely would increase chances of endorsement by governments. Alongside political support, corporate and residential level collaborations are essential to ensure the goal of conserving the Leopard by guaranteeing that conservation objectives are supported and upheld by local people (Zeller *et al.*, 2013). Because different areas within the region likely will present different challenges, conservation efforts should investigate and address these locally (Rabinowitz and Zeller, 2010).

7.5.3 *Reducing the illegal wildlife trade*

A broad array of measures is required to reduce the illegal wildlife trade in Southeast Asia, notably, it must be treated as serious crime, with allocation of sufficient resources, development and acquisition of appropriate technologies and equipment, as well as highly trained personnel that

effectively address the problem. Undoubtedly, improvements of law enforcement efforts are required, including intensified, more efficient, and data-informed patrolling schemes, larger number of rangers within protected areas (at least 5 rangers/100 km^2), as well as increments in frequency and coverage of patrolling efforts (Belecky and Gray, 2020). Alongside improvements of enforcement efforts, a holistic, multi-faceted approach is crucial to mitigate the snaring crisis, including development of effective incentives and other context-specific strategies that strive to reduce demand for wildmeat and a cessation snaring (Gray *et al.*, 2021). For that, enforced compliance mechanisms also are required, including the strengthening of the judicial system, with legislative reforms that criminalize non-traditional, commercialized poaching and possession of snares (including materials to build them), as well as the effective prosecution of offenders and adherence to the penalties proscribed by law (Belecky and Gray, 2020, Gray *et al.*, 2021, Gray *et al.*, 2018, Macdonald *et al.*, 2021).

The success combating the unprecedented pressures on wildlife, and ultimately protecting species will necessitate commitments and support from all governmental levels, non-governmental organisations, and society, as well as the strengthening of international legal cooperation to disrupt and dismantle wildlife trafficking in the region (Jiao *et al.*, 2021). To better understand and reduce the demand dynamics, intelligence-gathering operations that assess commodity chains are required (Ibbett *et al.*, 2020a). Overall, educational campaigns and engagement of local people are essential to reduce snaring and other illegal activities that promote wildlife decline within and around protected areas of the region. For instance, cultivating a network of reliable informants from local communities to supplement enforcement efforts could be beneficial, as these can provide additional information about poaching, thereby increasing patrol success, a strategy already shown to be advantageous in Indonesia (Linkie *et al.*, 2015).

Because most snaring is motivated by financial gain (MacMillan and Nguyen, 2014) and driven by the high demand for wildmeat, demand reduction efforts are required to decrease consumption of wildlife products by the general public. Social marketing and evidence-based behaviour change interventions can help reduce the demand for wildmeat and other wildlife products (Doughty *et al.*, 2021, Shairp *et al.*, 2016, Verissimo, 2013). Since socio-economic idiosyncrasies

appear to play a role in the persistence of Leopard (see Chapter 3), researchers can consider culturally relevant, faith-based strategies, when appropriate, as this likely would increase the potential for successful uptake. For example, behaviour change interventions that work in collaboration with places of worship (e.g., temple, mosque) potentially could help reduce the involvement in illegal wildlife trade and wildmeat consumption. A similar faith-based approach was implemented in Indonesia among Muslim communities through the issuing of the first ever Fatwa (Islamic law) or edict against illegal hunting and wildlife trafficking (Christy, 2014). This Fatwa also required Muslims to take an active role in protecting and conserving endangered species, while encouraging the government to review permits issued to environmentally harmful companies. The use of a faith-based approach has already benefited the Leopard in southern Africa, where members of the Nazareth Baptist "Shembe" Church, an amalgamation of traditional Zulu and Christian belief, began using synthetic Leopard skins instead of real skins for their ceremonies, which had represented both the principal cultural-religious use of illegal Leopard skins in the world and the biggest display of illegal wildlife contraband on earth (Liou, 2014, Naude *et al.*, 2020b). This culturally sensitive, faith-based approach could help reduce wildlife demand given the cultural overlaps between Buddhism/Taoism, Traditional Chinese Medicine, which is often affiliated with detrimental effects on wildlife, and wildmeat consumption in the region (Cheung *et al.*, 2021, Doughty *et al.*, 2019, Margulies *et al.*, 2019).

Infrastructural developments appear to be a relevant catalyst for illegal wildlife trade and overexploitation of natural resources by increasing access, connectivity and transport; thus, unless better regulated, these projects could soon intensify the severity and scale of the illegal trade in the region (Jiao *et al.*, 2021). Therefore, the potential impacts of future development projects occurring within or around protected areas need to be assessed before their implementation, including comprehensive and strategic environmental assessments that evaluate potential ecological and social impacts. This includes road developmental projects, as roads have been shown to not only promote illegal wildlife trade and act as precursors of overhunting and habitat destruction, but also to impede animal movement and incur direct negative impacts on wildlife, particularly large-bodied mammals such as Leopard (Clements *et al.*, 2014a, Oswell, 2010). If such projects are not adequately planned

and implemented, with strategies that reduce their environmental and societal impacts, remaining landscapes will become increasingly fragmented and stand to lose much of their wildlife and ecological integrity, bringing serious consequences to the wellbeing and economy of locals. Given that developmental projects will likely continue to increase in the region, it is imperative that measures are taken to minimise the impact on wildlife. Conservation initiatives should aim to find the mid-point between incorporating practices beneficial for wildlife conservation while not compromising on economic gains/societal wellbeing to increase the chances of endorsement by governments and other stakeholders.

7.5.4 *Funding*

A paramount barrier to improving the current situation of the Leopard and other wildlife in Southeast Asia is lack of funding. Currently, Leopard conservation in the region faces large budgetary shortfalls and inattention. In addition, the lack of concerted, efficient, long-term conservation efforts, together with high staff turnover within conservation NGOs, which oftentimes provide technical and financial support to the protected areas, have resulted in considerable losses of resources and effort (Gray *et al.*, 2012b). Several of these NGOs are restricted in their capacity to allocate resources, which frequently are bound by donors-specific requirements. This, in conjunction with limited economic investment from governments, has resulted in the lack of sufficient funding for several relevant activities. For example, law enforcement operations in the region are typically underfunded, reducing enforcement efforts, and often causing rangers, who work under difficult conditions (e.g., threatening encounters with poachers), to be poorly remunerated, insufficiently equipped, and inadequately trained, which in turn may increase chances of corruption (Belecky *et al.*, 2018, Ibbett *et al.*, 2020a, Ibbett *et al.*, 2020b, Long *et al.*, 2016).

A novel strategy to increase funding is to use imagery royalty of the species and other wildlife typical of the region (e.g., Tiger, Elephant; Courchamp *et al.*, 2018, Good *et al.*, 2017). Although several companies voluntarily support conservation projects (e.g., Cartier; Naude *et al.*, 2020b, Weller Sheppard, 2019), a mandatory royalty for wildlife imagery likely would aid in funding continuity of conservation projects, a major obstacle currently hampering conservation efforts in the

region. This approach has the potential not only to leverage funding, but also to aid in the shift of the current public perception that these species face no predicament if information on the species status is provided. That the public is largely ignorant about the imminent extinction risk of Leopard and other charismatic wildlife in the region is a biased perception which appears to be partially derived from product marketing campaigns that show off charismatic wildlife, without detailing the conservation status of these species, thereby unintendingly generating detrimental effects to the species conservation (Courchamp *et al.*, 2018). These unfavourable consequences can be compensated by channelling part of their associated profits to conservation. Some examples of products from which imagery royalty could be obtained due to their use of charismatic regional species include 'Leo Beer', 'Tiger Beer', and 'Chang beer' (Chang is the Thai word for Elephant), as well as Leopard print fashion designs (Good *et al.*, 2021). Amongst possible tactics previously identified to faster implement the royalty strategy is the creation of a third-party certification scheme, equivalent to 'Fairtrade' certification, that can be advertised on products that comply with the certification standards (Braczkowski, 2020). By using large felids as a model group, a previous study showed that by considering relevant companies on the Forbes 2000 list, between US$ 202 million and 2.02 billion potentially could be leveraged for conservation projects if these companies paid 0.1-1% of their profits in royalties (Braczkowski, 2020).

Another source of conservation funding is wildlife tourism. Likely due to the difficulty of observing animals in dense forests, wildlife tourism in Southeast Asia is not as popular and widespread as in Africa (Aihara *et al.*, 2016), yet this strategy potentially could be greatly expanded in the region (e.g., Cambodia). Aside from income generation, which can exceed the one-time consumptive revenues from extractive activities such as logging (Gwee *et al.*, 2019), wildlife tourism may entail several other benefits, including to act as deterrent of illegal human activities, and motivate authorities, rangers, and local people to protect wildlife (Lindsey *et al.*, 2017).

Due to the inherently changing landscapes (e.g., market, consumer landscape), complexity of human behavioural webs, and the characteristic heterogeneity of the region, several multi-faceted efforts, many of which are not mentioned here, will be required to change the current situation of the Leopard in the region. Conservation efforts would benefit greatly from a science-based prioritisation

protocol, with actions and resource allocation informed by knowledge gathered from systematic, long-term studies. The cumulative effect of several concerted regional interventions potentially would be greater than interventions implemented in isolation. Moreover, these concerted interventions likely would result in conservation effects beyond the protection of the species.

7.6 The bigger picture

Southeast Asia is a dynamic and heterogeneous region and the results obtained in this study provide a stark illustration of its characteristic diversity. However, this study supports previous findings that defaunation is becoming increasingly severe in the region, where a myriad of factors has facilitated the unsustainable levels of poaching currently evidenced in numerous areas, some of which were surveyed during this study. The incomparable and potentially irremediable detrimental effects of defaunation are diverse and include ecological, evolutionary, and socioeconomic impacts (Tilker *et al.*, 2019). For instance, defaunation not only causes population declines and drives species extinctions, but also results in homogenized and impoverished faunal communities, altering community- and ecosystem-level processes, and threatening the livelihoods of indigenous forest-dependent people (Tilker *et al.*, 2019). Given the ever-increasing demand for wildlife products and natural resources this trend is likely to become increasingly prevalent, augmenting the vulnerability of wildlife and contributing to expansion of the empty forest syndrome throughout the region. This is of particular concern from a conservation perspective, as the region, considered a major evolutionary hotspot for a diverse range of fauna and flora, harbours several endemic and unique species (de Bruyn *et al.*, 2014).

If the expanding economies and demands continue to exert unsustainable pressures on the ecosystems and wildlife, the latter will continue to suffer deterioration and declines. Unfortunately, as landscapes become more fragmented and densely populated, more extreme measures, such as full or partial fencing of some of the protected areas (Lindsey *et al.*, 2017), may be necessary to reduce the high levels of anthropogenic stressors within them.

7.7 Future directions for Leopard research and conservation in Southeast Asia

For both Leopard subspecies, further information is required about remaining populations not studied here; notably, within Myanmar and unprotected areas of Peninsular Malaysia for the Indochinese Leopard, and within most protected and unprotected areas for the Javan Leopard. Systematic monitoring of the remaining populations through repeated surveys are required to determine current status and allow for timely and effective actions. In addition, Leopard population trends need to be monitored closely, given that a slight increase in poaching can greatly increase the probability of extinction of Leopard, as it was reported for Tiger (Kenney *et al.*, 1995). Because the genetic and demographic consequences of poaching might not be immediately recognizable and extinction could occur years after poaching is reduced (Kenney *et al.*, 1995), these surveys could provide additional information about the health and viability of remaining populations. Camera-trap surveys likely represent the most effective tool to non-invasively study the characteristically low-density populations of the species in the region. The use of this monitoring tool has the added benefit of yielding large amounts of data from other non-target species, which can be used to investigate aspects of their ecology and conservation (e.g., see Appendix B, Appendix C and Appendix E), and inform comprehensive conservation strategies. Complementary survey methods, such as invertebrate-derived and environmental DNA, can increase detections of rare species and thus confidence of the estimates, particularly when surveying faunally impoverished systems (Abrams *et al.*, 2019, Tilker *et al.*, 2020).

In summary, certain aspects of Leopard ecology in the region remain unknown, including: a) ecology of the species during the wet season, b) degree of connectedness among populations, c) genetic diversity of populations, and d) quantification of the effects of snaring and other poaching methods on Leopard (e.g., sex and cohort survivorship). In addition, future research is needed to investigate the possibilities of restoring connectivity among populations. For that, the identification of unprotected populations and areas with dispersal potential is required, with careful consideration given to the local sociocultural circumstances when evaluating the probability of success for establishing a protected area or corridor.

The findings from this study suggest that, in spite of its resilience, the Leopard is not immune to anthropogenic pressures, especially poaching. Therefore, there is a clear need to delve deeper into the knowledge about the demand for and destination of Leopard and other wildlife parts in Southeast Asia and China, as well as site-specific motivations for snaring and other forms of poaching. This information will help relevant authorities and NGOs better plan for more efficient law enforcement operations and effective conservation strategies orientated towards increasing wildlife protection. Critically, evidence-based social interventions that strive to reduce the consumption and demand for wildmeat and other wildlife products are urgently required.

7.8 Concluding remarks

This thesis represents the most extensive study to date on Leopard conservation in Southeast Asia. Unfortunately, the level of deterioration of several populations throughout the region is such that it is pushing the Leopard, the epitome of adaptability, to the brink of extirpation. This study provides baseline data for the study areas, as well as new insights and advances using reliable and repeatable techniques, thereby improving knowledge of the species in the region, and facilitating future studies. Over the past few years, the outlook for the Leopard in Southeast Asia has worsened, and given the inherently changing landscape and fast developing economies in the region, the estimates provided here are likely to rapidly become optimistic. However, the region still holds potential for the long-term survival of Leopard if imminent action is taken to stem the current trend. Only with the implementation of timely and effective strategies will the Leopard have any chance of persisting in Southeast Asia.

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APPENDICES

Appendix A. *Panthera pardus* ssp. *delacouri*, Indochinese Leopard. The IUCN Red List of Red List of Threatened Species Assessment 2019.

Appendix B. Small cats in big trouble? Diet, activity, and habitat use of jungle cats and leopard cats in threatened dry deciduous forests, Cambodia.

Appendix C. Conservation status of large mammals in protected and logged forests of the greater Taman Negara Landscape, Peninsular Malaysia.

Appendix D. Big cats in borderlands: challenges and implications for transboundary conservation of Asian leopards.

Appendix E. Small carnivore records from Meru Betiri National Park, East Java.

Appendix F. *Panthera pardus*, Leopard. The IUCN Red List of Red List of Threatened Species Assessment 2016.

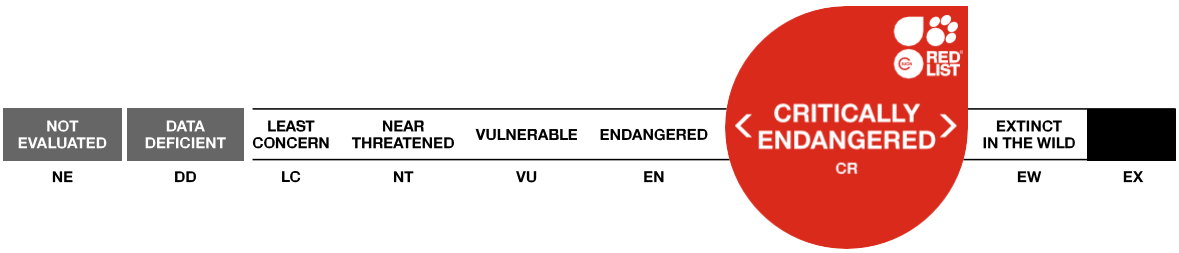
Appendix G. Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range.

Appendix A

The IUCN Red List of Threatened Species™
ISSN 2307-8235 (online)
IUCN 2019: T124159083A163986056
Scope(s): Global
Language: English

Panthera pardus ssp. *delacouri*, Indochinese Leopard

Assessment by: Rostro-García, S., Kamler, J.F., Clements, G.R., Lynam, A.J. & Naing, H.



View on www.iucnredlist.org

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Taxonomy

Kingdom	Phylum	Class	Order	Family
Animalia	Chordata	Mammalia	Carnivora	Felidae

Scientific Name: *Panthera pardus ssp. delacouri* Pocock, 1930

Parent Species: See *Panthera pardus*

Common Name(s):

- English: Indochinese Leopard
- Spanish; Castilian: Leopardo de Indochina
- French, Middle(ca.1400-1600): Léopard d'Indochine

Taxonomic Notes:

The Indochinese Leopard (*Panthera pardus delacouri*) has been classified as a separate subspecies based on genetic analyses (Miththapala *et al.* 1996, Uphyrkina *et al.* 2001) and its status as a subspeciesrecently was retained conservatively, pending further taxonomic investigation, in a review commissioned by the Cat Classification Task Force of the IUCN SSC Cat Specialist Group (Kitchener *et al.* 2017).

The distributional limits of *P. p. delacouri* are rather arbitrary, reflecting the paucity of critically validated specimens over much of the subspecies' putative range. Rostro-García *et al.* (2016) defined the Pearl River in southern China as the northern limit, and Singapore as the southern limit of the subspecies. In addition, the authors delineated the western border of Myanmar as the western limit of the subspecies, as suggested by Miththapala *et al.* (1996) and Uphyrkina *et al.* (2001). However, Kitchener *et al.* (2017) defined the western limit of the subspecies as the Irrawady river in Myanmar, with *P. p. fusca* occurring on the western side of the river. Because the revised taxonomy of the Felidaeby Kitchener *et al.* (2017) has been formally adopted as the current cat classification used by the IUCN SSC Cat Specialist Group and Red List Authority, the western limit of *P. p. delacouri* shown by Kitchener *et al.* (2017) is followed here.

Assessment Information

Red List Category & Criteria: Critically Endangered A2b+3b+4b ver 3.1

Year Published: 2019

Date Assessed: July 17, 2019

Justification:

The Indochinese Leopard is listed as Critically Endangered under criteria A2b+3b+4b, based on a suspected population decline greater than 80% over the last three generations, and that the causes of reduction have not ceased and may not cease in the future. The three generation period for assessment was considered to be about 22 years, based on the generation length of 7.4 years previously reported for the species (Stein *et al.* 2016). The Indochinese Leopard once ranged widely across Southeast Asia

and southeastern China (Nowell and Jackson 1996), but now occurs in only a small fraction (about 2%–6%) of its historical distribution (i.e. range prior to 1900). Remaining populations are small and isolated. This Leopard subspecies has been extirpated in Singapore, quite probably extirpated as a resident in Lao PDR and Viet Nam, nearly extirpated in Cambodia and China, and has a greatly reduced distribution in Thailand, Myanmar, and Malaysia. The main factor believed to be causing the dramatic decline of this subspecies, and leading to its disappearance from broad areas of otherwise suitable habitat, is increased poaching for the illegal wildlife trade, particularly intensive and indiscriminate snaring over large areas (Rostro-García *et al.* 2016). This threat is widespread and ongoing in Southeast Asia (Gray *et al.* 2018) and it is still causing declines in remaining Leopard populations (Rostro-García *et al*. 2018). The Leopard was the most frequently recorded species in a recent investigation about the trade of big cats in Myanmar and Thailand (Oswell 2010), and increased poaching is believed to be responsible for Leopard declines and extirpations in several areas (see population section). Otherpotential contributing factors to the present decline are habitat destruction, which facilitates poaching and promotes prey declines, and possibly disease. The deforestation rate in Southeast Asia is among thehighest in the world, and the habitat loss occurring in this region, as well as in China, has beenassociated with some of the highest levels of biodiversity loss in the world (Hughes 2017), which includes the Indochinese Leopard. Although a range-wide rate of population decline over the last three generations cannot be appropriately quantified, evidence from well-monitored localities indicates rapid ongoing declines where the Leopard still occurs in Southeast Asia. For example, Leopard densities decreased by 38% in three years at a site in Thailand (Simcharoen and Duangchantrasiri 2008), 44% in two years at a site in Malaysia (Hedges *et al.* 2015, Rimba unpubl. data), and 72% in five years at a site in Cambodia (Rostro-García *et al.* 2018) (see 'Population' for further detail). There is no obvious reason to assume that these localities are unrepresentative of Leopard population trend in Southeast Asia and adjacent China, nor that they represented anomalies in longer-term trends at the localities in question. All are consistent with a population decline in the last three generations exceeding 80%. On this basis, the taxon is categorised as Critically Endangered under A2b. In the face of the continuing threats, the population decline of the Indochinese Leopard is likely to persist unless immediate conservation actions are taken. Despite considerable investment in this taxon's range over the last two decades, the slow pace of conservation success gives little cause to suspect a region-wide major upswing over the next two decades. Notwithstanding the probability of some location-specific successes, this subspecies' recent rate of decline is likely to continue with little change, thus a further decline of 80% over the next three generations is suspected, qualifying it as Critically Endangered also under A3b and A4b.

Geographic Range

Range Description:

The geographic range of the Indochinese Leopard was recently described by Rostro-García *et al.* (2016). This assessment uses the data obtained by Rostro-García *et al.* (2016), and additional data collected since 2015 using the same methodologies.

Cambodia: Leopard now occurs in about 4% of the country, with an estimated range of around 7,932 km² (extant = 6,008 km², possibly extant = 1,924 km²). There appears to be only one remaining breeding population in the country, which is small and occurs within two protected areas of the Eastern Plains Landscape. In addition to that published by Rostro-García *et al.* (2016), the Leopard is now possibly extinct in the following five sites: Lomphat Wildlife Sanctuary, Keo Seima Wildlife Sanctuary, Chhlong area, Kien Svay District, and Prey Khieu Forest. The latter three sites are unprotected areas that have experienced

extensive human disturbance during the past 10 years, including land encroachment, logging, and poaching (Forestry Administration, unpubl. data), and it is unlikely that Leopard still occurs there. Within the Eastern Plains Landscape, Leopard has not been detected within Lomphat Wildlife Sanctuary and Keo Seima Wildlife Sanctuary during the past 10 years despite occasional camera trapping, during a period in which both protected areas experienced significant increases in land encroachment, logging, and poaching (WCS Cambodia and BirdLife International, unpubl. data). Although Leopard was detected in Chhep Wildlife Sanctuary (formerly Preah Vihear Protected Forest) in2013 and 2014 (Suzuki *et al.* 2017), it was not detected in 2015, suggesting that only a few individuals, if any, may occur there. Therefore, Chhep Wildlife Sanctuary is classified as possibly extant. In Srepok Wildlife Sanctuary (formerly Mondulkiri Protected Forest) and Phnom Prich Wildlife Sanctuary, both within the Eastern Plains Landscape, camera trap surveys detected Leopard in 2016 and 2018 (Panthera, WildCRU, WWF Cambodia and Ministry of Environment, unpubl. data), and this area is likely to contain the last remaining breeding population of Leopard in Cambodia. At these monitored localities recent steep population declines (see 'Population') suggest that the Leopard will probably be extirpated soon from both protected areas unless immediate conservation action is taken.

China: Leopard now occurs in less than 1% of southeastern China, with an estimated extant range of 2,483 km², as reported by Rostro-García *et al.* (2016). A recent review found the Indochinese Leopard was detected by camera traps only in two nature reserves, Nangunhe (2012–14) and Xishuangbanna (2008), both in southwestern Yunnan Province (Laguardia *et al.* 2017). Laguardia *et al.* (2017) concludedthat each locality contains only a few individuals (fewer than 10 individuals apiece) and populations areunlikely to recover because of low prey numbers, and high levels of habitat loss and poaching in the region. Thus, the Indochinese Leopard probably is on the verge of extirpation in the country (Rostro- García *et al.* 2016).

Lao PDR: There are unlikely to be any viable Leopard populations remaining in Lao PDR, and the Leopard is now likely to be functionally extinct in, if not fully extirpated from, the country (Rostro- García *et al.* 2016). Leopard was last photographed in 2004 in the Nam Et – Phou Louey (NEPL) National Protected Area, the largest and arguably best protected area in the country (Johnson *et al.* 2006), despite extensive camera-trapping and DNA testing of more than 500 scats since that time (WCS Lao PDR and Panthera, unpubl. data). Increases in snaring caused the extirpation of Tiger *Panthera tigris* in NEPL, the last remaining population of this species in Lao PDR (Johnson *et al.* 2016), and plausibly caused the extirpation of Leopard in NEPL as well. Although several areas of presumably suitable Leopard habitat in Lao PDR remain inadequately surveyed to know the status of the species within them, Leopard is unlikely to occur in a viable population within any of these areas, especially given that recent surveys have targeted the largest protected areas in the most remote regions of the country (e.g., NEPL and Nakai - Nam Theun National Protected Area). Leopard seemingly has disappeared from areas that appear to contain sufficient habitat and prey (e.g., NEPL), suggesting that local extirpations were likely to have been caused by poaching for the wildlife trade, similar to that observed in Cambodia (Rostro-García *et al.* 2016).

Malaysia: Leopard now occurs in about 36% of peninsular Malaysia (it did not occur in Borneo during historical times), with an estimated range of around 47,076 km² (extant = 12,365 km², possibly extant = 34,711 km²), as reported by Rostro-García *et al.* (2016). In contrast to other countries in Southeast Asia, Leopard still occurs throughout many forests in the country, including large complexes in the north (Belum-Temengor), central (Taman Negara), and south (Endau-Rompin), as well as in fragmented and secondary forests throughout the country (Rostro-García *et al.* 2016). Outside the three major protected-area complexes, Leopard was detected in 64% (9 of 14) of surveyed sites (Rostro-García *et al.*2016). Because most forested areas outside protected areas have not been surveyed, these areas were

categorised as possibly extant, unless Leopard was not detected in surveys within a specific site, given that poaching is presumed not to be as extensive as in other countries of Southeast Asia. Thus, peninsular Malaysia is considered one of the remaining strongholds for the Indochinese Leopard, although the populations are under threat from poaching. Recent increases in poaching in Malaysia might be causing considerable declines in Leopard numbers, similar to that reported for Tiger (Kawanishi 2015). At one of the best-monitored localities, Leopard numbers showed a recent steep decline (see 'Population'). In addition, there have been recent seizures of Leopard carcasses with snare marking in the country (TRAFFIC 2013) indicating snaring might be a considerable threat to Leopard in Malaysia.

Myanmar: Leopard now occurs in about 15% of its historical range in the country, with an estimated range of around 56,330 km² (extant = 13,217 km², possibly extant = 43,113 km²). From 1999 to 2004, Indochinese Leopard was detected in only 5 of 18 survey areas located throughout the country (Than Zaw *et al.* 2014), and its distribution is likely to have decreased since that time because of increased poaching, similar to that reported for Tiger in Myanmar (Lynam 2010). The Southern Forest Complex presumably contains the largest viable population of Leopard in the country (Rostro-García *et al.* 2016). This complex, which extends southwards in Myanmar to Lenya National Park, is contiguous with two large complexes in Thailand, which together comprise the Northern Tenasserim Forest Complex. Outside this complex, only one area, the northern Karen (Kayin) State, may hold a potentially viable population of Indochinese Leopard. This conclusion is based on recent Leopard records, size of area protected, prey availability, habitat quality, levels of human disturbance, and levels of effectiveenforcement**.**

Singapore: Leopard historically occurred in Singapore, but was extirpated from the island state as it developed (Corlett 1992).

Thailand: Leopard now occurs in about 5% of the country, with an estimated range of around 26,259 km² (extant = 16,196 km², possibly extant = 10,063 km²). Compared with that published by Rostro- García *et al.* (2016), we infer Leopard is now possibly extinct from the Khlong Saeng-Khao Sok Complexbecause extensive camera-trap surveys in 2017 did not detect Leopard in either Khlong Saeng Wildlife Sanctuary or Khlong Nakha Wildlife Sanctuary (Panthera, WildCRU, ZSL Thailand and DNPWPC, unpubl.data). In contrast, we included the Namtok Huai Yang National Park in the extant range because camera-trap surveys in 2017 recorded Leopard there (Freeland unpubl. data). We conclude that viable Leopard populations now occur in only 2 of 19 protected area complexes located in Thailand: Western Forest Complex (WEFCOM) and Kaeng Krachan-Kuiburi Complex (KKC). The KKC and WEFCOM, together with the Southern Forest Complex in Myanmar, comprise the Northern Tenasserim Forest Complex, which might contain the largest remaining population of Indochinese Leopard, and thus is considered one of the remaining strongholds for this subspecies. The WEFCOM is the largest complex in Thailand where Leopard still occurs, and within this complex Huai Kha Khaeng Wildlife Sanctuary is the best protected park (Duangchantrasiri *et al.* 2016) and probably has the highest Leopard density (Simcharoen and Duangchantrasiri 2008). However, Leopard was not detected in all protected areas that were adequately surveyed within WEFCOM (Rostro-García *et al.* 2016), indicating it might be underthreat within some protected areas that are part of the complex. Within KKC, Kuiburi National Park was reported to have relatively high Leopard densities (Steinmetz *et al.* 2009), although the current density is unknown. Outside these complexes, Leopard was recently detected in Hala Bala Wildlife Sanctuary (southern peninsula), and Salawin National Park (northwestern Thailand, Rostro-García *et al.* 2016). These protected areas, as well as the Namtok Huai Yang National Park (northern peninsula), are on theborder with Malaysia or Myanmar, and thus are part of larger transboundary populations.

Viet Nam: There are no known viable Leopard populations remaining in Viet Nam, and this species is now likely to have been extirpated from the country (Rostro-García *et al.* 2016). 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 areas (Rostro-García *et al.* 2016). The last published record of Leopard from Viet Nam was probably from the early 2000s in Yok Don National Park, in central Viet Nam (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 as a resident in Viet Nam given high levels of hunting and snaring there, which have devastated populations of smaller cat species in the country (Willcox *et al.* 2014).

The Indochinese Leopard occupies forest habitats down to sea-level. The upper altitudinal limit is not known. The Indian Leopard (*P. pardus fusca*) inhabits forests up to the tree line throughout the Himalayan region with a maximum elevation of 5,200 m (Nowell and Jackson 1996). Consequently, the Indochinese Leopard is likely to have occurred up to the tree line in northern Myanmar and adjacent areas of China, although no extant high altitude population is known.

Note: Additional data could result in an increase or decrease in population size or range loss of the Indochinese Leopard in certain areas.

Country Occurrence:

Native, Extant (resident): Cambodia; China; Malaysia; Myanmar; Thailand

Native, Possibly Extinct: Lao People's Democratic Republic; Viet Nam

Native, Extinct: Singapore

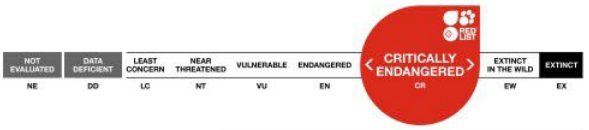
Distribution Map



Legend

- EXTANT (RESIDENT)
- POSSIBLY EXTANT (RESIDENT)
- POSSIBLY EXTINCT
- EXTINCT

Compiled by:
Rostro-García et al. 2019





The boundaries and names shown and the designations used on this map do not imply any official endorsement, acceptance or opinion by IUCN.

Population

The population of the Indochinese Leopard was estimated in 2015 to be 973–2,503 individuals, with 409–1,051 breeding adults (Rostro-García *et al.* 2016). However, Rostro-García *et al.* (2016) delineated the western limit of the Indochinese Leopard as the western border of Myanmar as suggested by Miththapala *et al.* (1996) and Uphyrkina *et al.* (2001), and therefore the estimate reported is not comparable with the present account. In this assessment, the Indochinese Leopard distribution was updated with the western limit delineated by Kitchener *et al.* (2017) and using additional data collected since 2015. In addition, the methodology used by Rostro-García *et al.* (2016) to estimate Leopard population size was modified. Following Rostro-García *et al.*(2016), we multiplied the area of distribution by an inferred density range. Results from previous camera-trap surveys across the region showed Leopard densities typically ranged from 0.5 to 4.9 Leopard/100 km² (Simcharoen and Duangchantrasiri 2008, Steinmentz *et al.* 2009, Gray and Prum 2012, Hedges *et al.* 2015, Rostro-García *et al.*2018, WildCRU, Panthera, WWF Cambodia and Ministry of Environment, unpubl. data). Therefore, we used a density range of 0.5–5.0 Leopard/100 km² for calculating the current population sizes within each country of its distribution. Because Leopard does not occupy sites uniformly when factors such asTiger densities, prey densities, habitat, and human disturbance are considered (Steinmetz *et al.* 2013, Carter *et al.* 2015), we calculated population size assuming 45% occupancy for areas within the currentdistribution. We selected 45% occupancy because it was the approximate midpoint of the range of occupancies reported in previous camera trap studies of Leopard in Asia (Carter *et al.* 2015, Steinmetz *et al.* 2013, WildCRU, Panthera, WWF Cambodia and Ministry of Environment, unpubl. data).

There are no robust estimates of the total number of mature Leopard individuals range-wide nor of the percentage of mature individuals in Leopard populations. Therefore, we followed the procedure used to estimate the percentage of mature individuals in populations of Snow Leopard (*Panthera uncia*, McCarthy *et al.* 2017), a species of the same genus. Leopard in the wild breeds first between 2 and 4 years of age (Balme *et al.* 2013), similar to that reported for Snow Leopard and other large cats (McCarthy *et al.* 2017). Therefore, we assumed that Indochinese Leopard is capable of breeding beginning at two years of age, and thus meets the IUCN definition of mature individual, even if no breeding occurs at this age. Population modelling for Snow Leopard showed that the most conservative estimate was a mean of 67.7% mature individuals in the population, based on when 2-year old maturity rates were lowest (25%), actual breeding did not begin until age 3-year, and the proportion of cubs in the population estimate was highest (50%, McCarthy *et al.* 2017). We assumed that percentage of mature individuals was similar in Indochinese Leopard populations, and therefore used 68% to estimatenumbers of mature individuals.

Following the IUCN Red List Guidelines (IUCN Standards and Petitions Subcommittee 2017), we estimated the total population in 2019 to be 114–1,130 individuals, including 77–766 mature individuals, based on the current extant range (i.e., possibly extant range was not included in the total population size) given within 'Distribution'.

An attempt was made to estimate the recent range-wide change in population, based on occupation of range, but this method was not suitable because of major differences between years in the mapping protocols. The only available distribution map of the Indochinese Leopard from about three generations ago showed a complete distribution across mainland Southeast Asia (Nowell and Jackson 1996). However, there were gaps in the Leopard distribution already by this time, because illegal hunting for

traditional medicine was already occurring throughout the region (Nowell and Jackson 1996). In addition, the main period of natural habitat loss in the range countries of the Indochinese Leopard hadalready occurred by the 1970s. Because information about where in Southeast Asia the Leopard was surviving was unavailable, the 1996 map cross-shaded all of mainland Southeast Asia, with the footnote 'abundance reduced, populations strongly localized'. Consequently, the distribution map of Nowell and Jackson (1996) cannot be compared with that made for this 2019 account to estimate the contraction of range within the region. The only updated map of Leopard distribution in Southeast Asia since 1996 is that published in the IUCN Red List assessment for the species in 2008 (Henschel *et al.* 2008). In this map extensive areas of Southeast Asia were retained as 'extant' although the Leopard waslikely to have been extirpated, or persisting in only highly fragmented populations across many areas of the region by that time (e.g. most of Lao PDR, Viet Nam and northern Thailand). Only the most obviously unsuitable areas were not shaded in this 2008 map, such as large agricultural or urban areas of the region. The 2019 Red List map was made using reliable, up-to-date information derived from an extensive review, which resulted in a more realistic, representation of Leopard distribution in SoutheastAsia and adjacent China than had been presented in 1996 or 2008. A shift from mapping areas with uncertainty from "benefit-of-the-doubt" presence to likely absent, precludes any meaningful quantification of the change in range occupancy between the current and previous maps. Although the severity of the decline in occupancy over the last three generations cannot appropriately be quantified, evidence from well-monitored localities indicates rapid ongoing declines where the Leopard still occurs in Southeast Asia. For example, in addition to the apparent extirpation of Leopard from Lao PDR and Viet Nam over the last three generations, there is ample and geographically wide-spread evidence that the remaining populations in the region are in steep ongoing decline. In Cambodia, the population in Srepok Wildlife Sanctuary declined by 72% from 2009 to 2014 because of increases in poaching (Rostro-García *et al.* 2018), along with a similar decrease in Phnom Prich Wildlife Sanctuary (WildCRU, Panthera, WWF Cambodia and Ministry of Environment, unpubl. data). In Kenyir Wildlife Corridor, adjacent to Taman Negara, Malaysia, there was a 100% turnover in the Leopard population over two years (2013–2015), which coincided with a 44% decline in density (Hedges *et al.* 2015, Rimba unpubl. data), indicating high mortality. Similarly, Leopard densities appeared to decrease by 38% in three yearsin Huai Kha Kaeng Wildlife Sanctuary, Thailand (Simcharoen and Duangchantrasiri 2008). There is no obvious reason to assume that these localities are unrepresentative of the overall Leopard population trend in Southeast Asia and adjacent China, nor that they represented anomalies in longer-term trends at the localities in question. All this information is consistent with a population decline in the last three generations exceeding 80%.

Note: Additional data could result in an increase or decrease in population size or range loss of the Indochinese Leopard in certain areas.
See Supporting Material for national population estimates of the Indochinese Leopard.

For further information about this species, see Supplementary Material.

Current Population Trend: Decreasing

Habitat and Ecology (see Appendix for additional information)

Habitat Types

The Indochinese Leopard is a habitat generalist and can occur in almost any habitat type in Southeast Asia, including primary and secondary forests, tropical dry and moist deciduous forests, evergreen and

semi-evergreen forests, and plantations. In Cambodia, China, and Thailand, Leopard distribution now is restricted to protected areas. In Malaysia and Myanmar, although primarily restricted to protected areas, Leopard also occurs in unprotected forests (Rostro-García *et al.* 2016) and even palm plantations(Azhar *et al.* 2014), although it is doubtful that viable populations occur in the latter habitat type.

Diet

Although Leopard preys preferentially upon species weighing 10–40 kg (Hayward *et al.* 2006), the diet of the Indochinese Leopard appears to vary according to habitat type, prey availability, and presence of larger carnivores. In protected areas in western Thailand, where Tiger was present and the main habitat was evergreen forest, the main prey of Leopard was primates, small to medium ungulates, and small carnivores (Rabinowitz 1989, Grassman 1999, Steinmetz *et al.* 2013, Lovari and Mori 2017). In contrast, in a protected area in eastern Cambodia that was dominated by open dry deciduous forests, and from which Tiger was recently extirpated, the main prey of Leopard was medium to large ungulates (Rostro-García *et al.* 2018). In fact, the main prey of Leopard in this population was Banteng (*Bos javanicus*), making this the only known Leopard population in the world that had main prey weighing greater than 500 kg (Rostro-García *et al.* 2018). Rostro-García *et al.* (2018) also showed that male Leopards, which can be 30–50% larger than female Leopards (Skinner and Chimimba 2005), had a different diet from that of females. Male Leopards consumed mostly Banteng, and preyed on all ungulates approximately in proportion to availability. In contrast, female Leopards consumed Northern Red Muntjac (*Muntiacus vaginalis*) more than expected, and avoided Banteng (Rostro-García *et al.* 2018). Leopard in other regions was shown to consume larger prey in the absence of larger carnivores (Harihar *et al.* 2011, Mondal *et al.* 2012, Stein and Hayssen 2013, Mann 2014), thus it was likely that after the extirpation of Tiger, male Leopard in eastern Cambodia expanded its dietary niche, and consumed large prey such as Banteng. Overall, the dietary studies of the Indochinese Leopard showed ahighly varied diet, with prey ranging in size from insects to Banteng, owing to the opportunistic nature of the species.

Home Ranges and Activity

Home range size of Leopard varies with prey availability, habitat types, age, and season. Also, male home ranges tend to be larger than females at any given site. For the Indochinese Leopard, home ranges have been determined only for radio-collared individuals in western Thailand. In Huai Kha Khaeng Wildlife Sanctuary, home ranges varied from 27–56 km² for males and 11–41 km² for females (Rabinowitz 1989, Simcharoen *et al.*2008). In Kaeng Krachan National Park, home ranges were 17–18 km² for two males and 9 km² for one female (Grassman 1999). Subadult females were found to reside within their respective mother's territories and had home ranges within the general size range of adult females (Simcharoen *et al.* 2008). These studies showed that home ranges increased significantly during the wet season for males, but not for females (Rabinowitz 1989, Grassman 1999, Simcharoen *et al.* 2008).

In protected areas in western Thailand, Indochinese Leopard activity was found to be either arrhythmic or mostly diurnal and crepuscular (Rabinowitz 1989, Grassman 1999, Ngoprasert *et al.* 2007). In contrast, Leopard in eastern Cambodia was found to be mostly nocturnal (WildCRU, Panthera, WWF Cambodia and Ministry of Environment unpubl. data) probably due to higher levels of human activity and persecution compared with those in the protected areas in Thailand.

Densities

Reported densities of the Indochinese Leopard range from 1.0 to 7.9 Leopards/100 km² (Simcharoen and Duangchantrasiri 2008, Rostro-García *et al.*2018). In Cambodia, densities in Srepok Wildlife Sanctuary ranged from 3.6 Leopards/100 km² in 2009 (Gray and Prum 2012) to 1.0 Leopards/100 km² in 2014 (Rostro-García *et al.*2018). In Malaysia, densities in Kenyir Wildlife Corridor, adjacent to Taman Negara, Malaysia, ranged from 3.0 Leopards/100 km² in 2013 (Hedges *et al.*2015) to 1.7 Leopards/100 km² in 2015 (Rimba, unpubl. data). In Thailand, densities have been estimated to be 7.9 Leopards/100 km² in 1996 and 4.9 Leopards/100 km² 1999 in Huai Kha Kaeng Wildlife Sanctuary (Simcharoen and Duangchantrasiri 2008), and to range from 3.3 to 4.8 Leopards/100 km² in 2007 and 2009, respectively, in Kuiburi National Park (Steinmetz *et al.* 2009). Overall, densities of the Indochinese Leopard appear to be strongly affected by the poaching of Leopard and its prey, thus the density of Leopard in the absence of these human impacts is unknown.

Melanism

In contrast to all other mainland Leopard subspecies throughout the world, the Indochinese Leopard is unique in that a large percentage of remaining individuals are melanistic, including nearly 100% of the individuals in the Malay Peninsula (Kawanishi *et al.* 2010). The exceptions are the populations of the Indochinese Leopard in the open dry deciduous forests of eastern and northern Cambodia, in which all individuals are spotted. It has been hypothesized that melanism in the Indochinese Leopard was an adaptation to the closed canopy of tropical evergreen forests in Southeast Asia, thereby allowing better concealment of Leopard to ambush prey or avoid dominant Tiger in shadowy habitats where light seldom penetrates to the forest floor (Kawanishi *et al.* 2010). More recent research suggests that melanism is an adaptation in Leopard that helps with thermoregulation in hot humid forests in addition to camouflage (da Silva *et al.* 2017), thus there may be multiple benefits for the same gene expression. Both hypotheses would explain why melanism is absent from Indochinese Leopard inhabiting northern and eastern Cambodia, because these forests are both open and dry. That melanism is present in a large percentage of the Indochinese Leopard individuals, and that overall this adaptation appears positively selected for in a tropical region to help with thermoregulation and/or camouflage, suggests this subspecies could have other unique adaptations that are less visible than melanism.

Systems: Terrestrial

Use and Trade

The Indochinese Leopard is killed illegally for the wildlife trade in Southeast Asia and southeastern China for its body parts, particularly bones and meat, which are used in traditional Asian medicine (Oswell 2010, Raza *et al.* 2012). Other Leopard parts, such as teeth and skins, are sold as amulets or decorative items. Leopard was the most frequently recorded species in a recent investigation about the trade of big cats in Myanmar and Thailand, with a minimum of 167 individuals recorded in trade in a period of less than 10 years (Oswell 2010). The two main destinations for Leopard parts in Southeast Asia appear to be China and Viet Nam (Rostro-García *et al.* 2016), although constant trade to Korea and Taiwan also has been reported (Oswell 2010). However, more information is needed about the demand for and destination of Leopard parts in Southeast Asia and China, so that governments can plan more efficient law enforcement operations and non-governmental organisations can initiate effective campaigns orientated towards reducing demand.

Threats **(see Appendix for additional information)**

Poaching for the illegal wildlife trade is likely to be the greatest factor contributing to the decline of the Indochinese Leopard. Leopard body parts, particularly bones and meat, can be used in traditional Asian medicine, and other Leopard parts, such as teeth and skins, can be sold as luxury items (Oswell 2010, Raza *et al.* 2012). Therefore, Leopard is targeted by poachers, particularly when Tiger numbers are low. A snaring crisis is occurring throughout Southeast Asia, which is driving severe declines in many species, even within protected areas (Gray *et al.* 2017, 2018). The primary reason for snaring is to acquire wild meat for the commercial bushmeat trade (Ripple *et al.* 2016), which often targets common ungulate species such as Wild Pig (*Sus scrofa*) and Muntjacs (*Muntiacus* spp.). However, snares are unselective and generate substantial by-catch, resulting in the capture of non-target species (Ripple *et al.* 2016), including Leopard. The widespread intensive snaring for the commercial bushmeat trade probably is causing most of the current human-driven mortality of Leopard. Poaching, either direct or as by-catch, is likely to have led to the disappearance of this subspecies from broad areas of otherwise suitable habitat in Southeast Asia.

Other potential factors contributing to the recent Leopard decline in Southeast Asia and southeastern China are habitat destruction, which facilitates poaching and prey declines, and possibly disease. Habitat loss and fragmentation are probably nowadays only indirect threats to the Leopard in most areas of Southeast Asia, because these factors are closely associated with high levels of human disturbance and poaching. For example, 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). The deforestation rate in Southeast Asia has been one the highest of all tropical regions, with much of it inside protected areas (Heino *et al.* 2015), and deforestation rates were still accelerating as of 2010 (Sodhi *et al.* 2010, Miettinen *et al.* 2011, Kim *et al.* 2015). The primary drivers of deforestation in the region are land conversion for plantations (Miettinen *et al.* 2011, Wilcove *et al.* 2013) and croplands(Carter *et al.* 2017, Zeng *et al.* 2018). For example, the area of primary or secondary forests combined decreased in all Southeast Asian countries from 2000 to 2010, most of which was because of conversionto 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 less than 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 indirect impacts on Leopard populations. In addition, Southeast Asia is a densely populated and rapidly developing region, thus human settlement encroachment and expanding agricultural lands (Carter *et al.* 2017, Zeng *et al.* 2018) also are threats to Leopard. Consequently, even if snaring within protected areas was to be suppressed, habitat loss and fragmentation could become a problem for the already small and isolated populations of Leopard.

Prey depletion, while unlikely to have driven the range collapse of the Leopard given its generalist and opportunistic nature (Hayward *et al.* 2006, Rostro-García *et al.* 2018), might be a factor that hinders Leopard recovery. Throughout Southeast Asia and southeastern China, populations of non-human primates and large ungulates, typical prey of Leopard in the region (Rabinowitz 1989, Grassman 1999, Rostro-García *et al.* 2018), are well below carrying capacity because of overhunting by humans, even within protected areas (Johnson *et al.* 2006, Steinmetz *et al.* 2010, Kawanishi *et al.* 2013, Hla Naing *et al.* 2015). Thus, even in the (at present, hypothetical) absence of poaching of the Indochinese Leopard, the subspecies might not survive competition with humans if its prey base continues to be depleted by overhunting.

Disease, especially canine distemper virus (CDV), might be another factor negatively affecting Leopard populations in some areas of the region. Although not originally thought to be common in cat species, CDV outbreaks have increasingly been shown to devastate local Panthera populations during the past 20 years (Roelke-Parker *et al.* 1996, Gilbert *et al.* 2015). The CDV has been confirmed in wild Amur Leopard (*P. pardus orientalis*, Sulikhan *et al.* 2018), and might increase extinction rates in small isolated Leopard populations, similar to that shown for Tiger (Gilbert *et al.* 2014). Importantly, CDV outbreaks in Panthera populations typically originate in local village dogs (Roelke-Parker *et al.* 1996), thus prohibitionof dogs from protected areas in Southeast Asia might be necessary to prevent the transmission of diseases. However, more information is needed on the prevalence of CDV in Indochinese Leopard, and the potential impact this disease might have on small Leopard populations.

In contrast to other Leopard subspecies, conflict with humans is not a major threat to Indochinese Leopard. Attacks on livestock or humans are rarely reported in the region, presumably because densities of Indochinese Leopard are too low to cause significant or widespread conflict. In contrast to Africa, legal trophy hunting does not occur in Southeast Asia, thus this factor is not a threat to Indochinese Leopard.

Conservation Actions **(see Appendix for additional information)**

The Leopard is included in CITES Appendix I and in CMS Appendix II. The Leopard is legally protected in China and all countries in Southeast Asia. However, regular enforcement of national laws and patrolling strategies within protected areas are insufficient to provide effective protection of Indochinese Leopard throughout most of the remaining range. For example, in Nam Et – Phou Louey National Protected Area, northern Lao PDR, an increase in funding for enforcement resulted in an increase of days patrolled over a 7-year period, which positively affected gun confiscations and arrest of poachers, but it ultimately failed to prevent the extirpation of Tiger and Leopard because the proliferation of snares was not stopped (Johnson *et al.* 2016). The development of a systematic, intensified, and effective enforcement regime helped maintain Tiger numbers in Huai Kha Kaeng (Duangchantrasiri *et al.* 2016). This enforcement strategy is likely to benefit the Leopard as well, therefore similar enforcement strategies are recommended for other protected areas in Southeast Asia and southeastern China where the Indochinese Leopard still occurs. In general, a broad array of actions is required to stem the illegal wildlife trade, including increasing the number of rangers and anti-poaching units, ensuring effective deterrents, coinciding with proactive enforcement, and increases in patrols and check-points to preventpoachers from entering the protected areas. Importantly, given the snaring crisis occurring throughout Southeast Asia, enforcement regimes must address snare removal and prevention, which ultimately means engaging with communities that are the source of the snaring. Likewise, transboundary collaborations among relevant bodies need to be improved to reduce illegal wildlife trade and enhance Leopard conservation (Farhadinia *et al*. 2020). Even if poaching is suppressed, fragmentation of Leopard populations could remain a problem. Many of the protected areas that still harbour Indochinese Leopard are isolated, which might hinder the maintenance of genetically viable populations (Kenney *et al.* 2014). Therefore, to ensure the survival of a viable Leopard metapopulation in the long term, the connectivity of subpopulations must be secured through establishing or maintaining corridors (Kenney *et al.* 2014). Other conservation actions needed to recover Leopard populations in Southeast Asia and southeastern China should include the conservation and recovery of the main prey species, and the prohibition of dogs from protected areas, to prevent the transmission of CDV and other diseases. Community outreach has been shown to be effective in reducing poaching and increasing prey populations inside Kuiburi National Park, western Thailand (Steinmetz et al. 2014), thus similar programmes should be implemented in other comparable protected areas throughout the region.

Overall, education campaigns also are necessary to reduce demand for bushmeat and wildlife parts at the provincial, national, and regional levels (Gray *et al.* 2018). Despite the precarious state of the Indochinese Leopard across its range, there are no conservation measures or monitoring programmes specifically focused on this subspecies, except for the long-term monitoring of the Leopard population in eastern Cambodia (WildCRU, Panthera, WWF Cambodia, and Ministry of Environment), and Taman Negara National Park/Kenyir Wildlife Corridor in Malaysia (Rimba, Panthera, Woodland Park Zoo, and DWNP). From 2015 to 2018, Panthera established a Southeast Asia section for their Leopard Program with the goal of establishing long-term monitoring sites in key populations throughout Southeast Asia. Finally, we recommend the development of a coordinated captive breeding programme for the Indochinese Leopard among zoos in Southeast Asia. Although the total number in captivity is unknown, Indochinese Leopard occurs in many zoos throughout Southeast Asia, including Cambodia, Lao PDR, Thailand, Malaysia, Myanmar, Singapore, and Viet Nam (J. Kamler pers. obs.). However, there is no coordinated captive breeding programme for the Indochinese Leopard. Such a programme is necessary to preserve the genetic integrity of captive Indochinese Leopard, which ultimately may be the source of any potential reintroductions in the future.

Credits

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External Resources

For Supplementary Material, and for Images and External Links to Additional Information, please see the Red List website.

Appendix

Habitats

(http://www.iucnredlist.org/technical-documents/classification-schemes)

Habitat	Season	Suitability	Major Importance?
1. Forest -> 1.5. Forest - Subtropical/Tropical Dry	Resident	Suitable	Yes
1. Forest -> 1.6. Forest - Subtropical/Tropical Moist Lowland	Resident	Suitable	Yes
1. Forest -> 1.7. Forest - Subtropical/Tropical Mangrove Vegetation Above High Tide Level	Resident	Suitable	Yes
1. Forest -> 1.8. Forest - Subtropical/Tropical Swamp	Resident	Suitable	Yes
1. Forest -> 1.9. Forest - Subtropical/Tropical Moist Montane	Resident	Suitable	Yes
3. Shrubland -> 3.5. Shrubland - Subtropical/Tropical Dry	Resident	Suitable	-
3. Shrubland -> 3.6. Shrubland - Subtropical/Tropical Moist	Resident	Suitable	-
3. Shrubland -> 3.7. Shrubland - Subtropical/Tropical High Altitude	Resident	Suitable	-
4. Grassland -> 4.5. Grassland - Subtropical/Tropical Dry	Resident	Marginal	-
14. Artificial/Terrestrial -> 14.3. Artificial/Terrestrial - Plantations	Resident	Marginal	-

Use and Trade

(http://www.iucnredlist.org/technical-documents/classification-schemes)

End Use	Local	National	International
Food - human	Yes	No	No
Wearing apparel, accessories	Yes	No	No
Handicrafts, jewellery, etc.	Yes	No	No
Medicine - human & veterinary	Yes	No	No

Threats

(http://www.iucnredlist.org/technical-documents/classification-schemes)

Threat	Timing	Scope	Severity	Impact Score
5. Biological resource use -> 5.1. Hunting & trapping terrestrial animals -> 5.1.1. Intentional use (species is the target)	Ongoing	-	Rapid declines	Low impact: 5
	Stresses:	2. Species Stresses -> 2.1. Species mortality		

5. Biological resource use -> 5.1. Hunting & trapping terrestrial animals -> 5.1.2. Unintentional effects (species is not the target)	Ongoing	-	Rapid declines	Low impact: 5
	Stresses:	2. Species Stresses -> 2.1. Species mortality		

Conservation Actions in Place

(http://www.iucnredlist.org/technical-documents/classification-schemes)

Conservation Action in Place
In-place research and monitoring
Action Recovery Plan: No
Systematic monitoring scheme: No
In-place land/water protection
Conservation sites identified: Yes, over entire range
Area based regional management plan: No
Occurs in at least one protected area: Yes
Invasive species control or prevention: No
In-place species management
Harvest management plan: No
Successfully reintroduced or introduced benignly: No
Subject to ex-situ conservation: No
In-place education
Included in international legislation: Yes
Subject to any international management / trade controls: Yes

Conservation Actions Needed

(http://www.iucnredlist.org/technical-documents/classification-schemes)

Conservation Action Needed
2. Land/water management -> 2.2. Invasive/problematic species control
2. Land/water management -> 2.3. Habitat & natural process restoration
3. Species management -> 3.4. Ex-situ conservation -> 3.4.1. Captive breeding/artificial propagation
3. Species management -> 3.4. Ex-situ conservation -> 3.4.2. Genome resource bank
4. Education & awareness -> 4.2. Training
4. Education & awareness -> 4.3. Awareness & communications

Conservation Action Needed
5. Law & policy -> 5.4. Compliance and enforcement -> 5.4.1. International level
5. Law & policy -> 5.4. Compliance and enforcement -> 5.4.2. National level
5. Law & policy -> 5.4. Compliance and enforcement -> 5.4.3. Sub-national level
5. Law & policy -> 5.4. Compliance and enforcement -> 5.4.4. Scale unspecified

Research Needed

(http://www.iucnredlist.org/technical-documents/classification-schemes)

Research Needed
1. Research -> 1.1. Taxonomy
1. Research -> 1.2. Population size, distribution & trends
1. Research -> 1.5. Threats
1. Research -> 1.6. Actions
2. Conservation Planning -> 2.1. Species Action/Recovery Plan
3. Monitoring -> 3.1. Population trends
3. Monitoring -> 3.2. Harvest level trends
3. Monitoring -> 3.3. Trade trends

Additional Data Fields

Distribution
Estimated area of occupancy (AOO) (km²): 50270
Continuing decline in area of occupancy (AOO): Yes
Extreme fluctuations in area of occupancy (AOO): No
Population
Number of mature individuals: 77-766
Extreme fluctuations: No
Population severely fragmented: No
Extreme fluctuations in subpopulations: No
All individuals in one subpopulation: No
Habitats and Ecology
Generation Length (years): 7.4

The IUCN Red List Partnership



The IUCN Red List of Threatened Species™ is produced and managed by the IUCN Global Species Programme, the IUCN Species Survival Commission (SSC) and The IUCN Red List Partnership.

The IUCN Red List Partners are: Arizona State University; BirdLife International; Botanic Gardens Conservation International; Conservation International; NatureServe; Royal Botanic Gardens, Kew; Sapienza University of Rome; Texas A&M University; and Zoological Society of London.

Appendix B

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ORIGINAL RESEARCH

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Small cats in big trouble? Diet, activity, and habitat use of jungle cats and leopard cats in threatened dry deciduous forests, Cambodia

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Abstract

Dry deciduous dipterocarp forests (DDF) cover about 15%–20% of Southeast Asia and are the most threatened forest type in the region. The jungle cat (*Felis chaus*) is a DDF specialist that occurs only in small isolated populations in Southeast Asia. Despite being one of the rarest felids in the region, almost nothing is known about its ecology. We investigated the ecology of jungle cats and their resource partitioning with the more common leopard cats (*Prionailurus bengalensis*) in a DDF-dominated landscape in Srepok Wildlife Sanctuary, Cambodia. We used camera-trap data collected from 2009 to 2019 and DNA-confirmed scats to determine the temporal, dietary and spatial overlap between jungle cats and leopard cats. The diet of jungle cats was relatively diverse and consisted of murids (56% biomass consumed), sciurids (15%), hares (*Lepus peguensis*; 12%), birds (8%), and reptiles (8%), whereas leopard cats had a narrower niche breadth and a diet dominated by smaller prey, primarily murids (73%). Nonetheless, dietary overlap was high because both felid species consumed predominantly small rodents. Both species were primarily nocturnal and had high temporal overlap. Two-species occupancy modelling suggested jungle cats were restricted to DDF and had low occupancy, whereas leopard cats had higher occupancy and were habitat generalists. Our study confirmed that jungle cats are DDF specialists that likely persist in low numbers due to the harsh conditions of the dry season in this habitat, including annual fires and substantial decreases in small vertebrate prey. The lower occupancy and more diverse diet of jungle cats, together with the broader habitat use of leopard cats, likely facilitated the coexistence of these species. The low occupancy of jungle cats in DDF suggests that protection of large areas of DDF will be required for the long-term conservation of this rare felid in Southeast Asia.

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Appendix C

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Conservation status of large mammals in protected and logged forests of the greater Taman Negara Landscape, Peninsular Malaysia

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Abstract. *Clements GR, Rostro-García S, Kamler JF, Liang SH, Hashim AKBA. 2021. Conservation status of large mammals in protected and logged forests of the greater Taman Negara Landscape, Peninsular Malaysia. Biodiversitas 22: 272-277.* Peninsular Malaysia contains a large community of IUCN Threatened mammal species, although recent records in some protected areas is unknown. The greater Taman Negara Landscape is one of the national priority areas for tiger conservation, but the recent occurrence of large mammals in the landscape has not been sufficiently updated. Here, we conducted systematic camera-trap surveys in protected and logged forests of the Taman Negara Landscape: Merapoh in Taman Negara National Park (TNM), and the Dungun Timber Complex (DTC), respectively. We found that the diversity of large mammals in TNM appeared to be the same between 2000 and 2016. The detection frequencies (DF) of several Threatened species, such as Malayan tiger (*Panthera tigris jacksoni*), dhole (*Cuon alpinus*), and Malayan pangolin (*Manis javanica*), were similar between surveys, suggesting the relative abundance of these species likely remained stable during the past 16 years. However, the DF of Asian elephant (*Elephas maximus*) and Malayan tapir (*Tapirus indicus*) were lower compared to 2000. In DTC, overall mammalian diversity was relatively lower than in TNM, primarily due to the non-detection of two large ungulates: gaur (*Bos gaurus*) and sambar (*Rusa unicolor*). Nevertheless, we recorded several other Threatened species of mammals, suggesting there is potential for this forest reserve to preserve some of Peninsular Malaysia's most Threatened mammal species. Our results suggest that the Taman Negara Landscape is still an important global site for the conservation of several Threatened species, and we recommend an increase in wildlife law enforcement efforts to ensure the survival of its large and diverse mammalian community.

Keywords: Biodiversity, carnivores, large mammals, Malaysia, Taman Negara National Park

INTRODUCTION

Large mammals have experienced steep declines throughout Southeast Asia, and many are now listed as Threatened species by the IUCN. Large apex carnivores, in particular, have exhibited massive range contractions in Southeast Asia, including tiger (*Panthera tigris;* Lynam and Nowell 2011; Kawanishi 2015), leopard (*P. pardus*; Rostro-García et al. 2019), and dhole (*Cuon alpinus*; Kamler et al. 2015). The primary reasons for the declines include poaching for the illegal wildlife trade, habitat loss, and prey declines (Kamler et al. 2015; Kawanishi 2015; Rostro-García et al. 2018). Similarly, large ungulates also have experienced density declines and large range contractions in Southeast Asia, such as gaur (*Bos gaurus*; Duckworth et al. 2016), and sambar (*Rusa unicolor*; Timmins et al. 2015), mainly due to poaching and habitat loss.

Peninsular Malaysia harbors several highly threatened mammal species, including the Critically Endangered Malayan tiger (*P. tigris jacksoni*), Critically Endangered Indochinese leopard (*P. pardus delacouri*), Endangered dhole, Endangered Asian elephant (*Elephas maximus*), Endangered Malayan tapir (*Tapirus indicus*), and the Critically Endangered Malayan pangolin (*Manis javanica*). Other Mammalian species listed as Vulnerable within Peninsular Malaysia include the mainland clouded leopard (*Neofelis nebulosa*), sun bear (*Ursus malayanus*), binturong (*Arctictis binturong*), southern pig-tailed macaque (*Macaca nemestrina*), Sumatran serow (*Capricornis sumatraensis*), gaur, and sambar. Clearly, Peninsular Malaysia contains a large community of Threatened species with vastly different body sizes and ecological needs. Large protected areas containing diverse habitats likely offer the best hope for conserving such a wide variety of Threatened species in Peninsular Malaysia.

Taman Negara National Park (4,343 km^2, hereafter Taman Negara), established in 1938-39, is Peninsular Malaysia's largest protected area, and one of the largest protected areas in Southeast Asia. The biodiversity of Taman Negara is high; camera-trap surveys in three different grids in 2000 recorded >30 mammal species >1 kg (Kawanishi and Sunquist 2004). That survey confirmed that Taman Negara, at that time, contained all the mammal

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Appendix D

Forum

Big cats in borderlands: challenges and implications for transboundary conservation of Asian leopards

Mohammad S. Farhadinia, Susana Rostro-García, Limin Feng
Jan F. Kamler, Andrew Spalton, Elena Shevtsova, Igor Khorozyan
Mohammed Al-Duais, Jianping Ge and David W. Macdonald

Abstract Large carnivores have extensive spatial requirements, with ranges that often span geopolitical borders. Consequently, management of transboundary populations is subject to several political jurisdictions, often with heterogeneity in conservation challenges. In continental Asia there are four threatened leopard subspecies with transboundary populations spanning 23 countries: the Persian *Panthera pardus saxicolor*, Indochinese *P. pardus delacouri*, Arabian *P. pardus nimr* and Amur *P. pardus orientalis* leopards. We reviewed the status of these subspecies and examined the challenges to, and opportunities for, their conservation. The Amur and Indochinese leopards have the majority (58–100%) of their remaining range in borderlands, and the Persian and Arabian leopards have 23–26% of their remaining ranges in borderlands. Overall, in 18 of 23 countries the majority of the remaining leopard range is in borderlands, and thus in most countries conservation of these subspecies is dependent on transboundary collaboration. However, we found only two transboundary initiatives for Asian leopards. Overall, we highlighted three key transboundary landscapes in regions that are of high importance for the survival of these subspecies. Recent listing of the leopard in the Bonn Convention on the Conservation of Migratory Species of Wild Animals is important, but more international collaboration is needed to conserve these subspecies. We provide a spatial framework with which range countries and international agencies could establish transboundary cooperation for conserving threatened leopards in Asia.

Keywords Asia, Bonn Convention on the Conservation of Migratory Species of Wild Animals, borderland, conservation geopolitics, leopard, *Panthera pardus*, security fence, transboundary

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Introduction

Large carnivores have extensive spatial requirements that may extend beyond geopolitical borders. Consequently, these wide-ranging animals can fall under several political jurisdictions, resulting in a diversity of conservation challenges and efforts (Bischof et al., 2016; Linnell et al., 2016). Neighbouring states may have different levels of technical expertise, knowledge, capacity and financial resources (Karlstetter & Mallon, 2014). Importantly, persistence of large carnivore populations in one country can depend, because of source–sink dynamics, on populations on the other side of an international border (Falcucci et al., 2013; Farhadinia et al., 2015; Feng et al., 2017). Conservation of large carnivores requires a holistic appreciation of the geopolitical context (Hodgetts et al., 2019) for maintaining source populations as a priority and, where possible, enhancing links to ensure persistence of metapopulations.

Although geopolitical borderlands are typically rich in biodiversity, protecting these landscapes is often challenging. National conservation programmes usually stop at international borders, but the species they aim to conserve and the threats they strive to halt often do not (Macdonald et al., 2018). Borderlands are characterized by dynamic social, political, economic and sometimes even ecological transitions that, at extremes, may involve armed conflict and political instability (McNeely, 2003). Man-made barriers along geopolitical borders, intended to control

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Appendix E

IUCN/SSC Small Carnivore Specialist Group

ARTICLE

Small carnivore records from Meru Betiri National Park, East Java

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Abstract

A camera-trap survey was conducted from August to November 2017 in Meru Betiri National Park, East Java. Photographs of Binturong *Arctictis binturong* represent the most southern global record and extend the known range about 500 km farther east in Java than is currently portrayed. Photographs of Yellow-throated Marten *Martes flavigula* are the most eastern record of the endemic Javan subspecies *M. f. robinsoni*. Other small carnivore species recorded were the Javan Ferret Badger *Melogale orientalis*, Javan Mongoose *Herpestes javanicus*, Leopard Cat *Prionailurus bengalensis* and Common Palm Civet *Paradoxurus hermaphroditus*.

Keywords: Viverridae, Mustelidae, Herpestidae, Prionodontidae, tropical lowland forest, wildlife conservation, camera-trapping

Introduction

The Binturong *Arctictis binturong* reportedly has a distribution that extends from eastern Nepal and southern China, southwards to Sumatra, Borneo and western Java (Willcox *et al.* 2015). The Binturong is listed as Vulnerable in The IUCN Red List of Threatened Species because of population declines through hunting and habitat loss, and this species is now uncommon or rare throughout much of its distribution (Willcox *et al.* 2015). Records of Binturong in Java are rare; transect surveys recorded this species from only two localities in western Java, whereas four sites in East Java, including Meru Betiri National Park, failed to detect this species (Rode-Margono et al. 2014). Consequently, the distribution of Binturong on Java was considered to be restricted to western Java (Fig. 1; Willcox *et al.* 2015).

The Yellow-throated Marten *Martes flavigula* has a wide distribution that extends from Afghanistan to the Russian Far East, south to Sumatra, Borneo and parts of Java (Chutipong *et al.* 2016a). This species is listed as Least Concern, reflecting its evidently large population and its tolerance for a wide range of habitats, including degraded forests (Chutipong *et al.* 2016a). The Javan endemic subspecies *M. f. robinsoni* is clearly distinct from martens on Peninsular Malaysia, Borneo and Sumatra, and might even warrant classification as a distinct species (Schreiber *et al.* 1989). The status and distribution of the Javan endemic subspecies is poorly known, and Chutipong et al. (2016a) suggested that it might be threatened. Published records of the Yellow-throated Marten in Java are rare (e.g. Rode-Margono *et al.* 2014), but various unpublished records (e.g. J. A. Eaton in Chutipong *et al.* 2016a) suggest

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Appendix F

The IUCN Red List of Threatened Species™
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Assessment can be accessed at: https://www.iucnredlist.org/species/15954/163991139

Appendix G

PeerJ

Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range

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ABSTRACT

The leopard's (*Panthera pardus*) broad geographic range, remarkable adaptability, and secretive nature have contributed to a misconception that this species might not be severely threatened across its range. We find that not only are several subspecies and regional populations critically endangered but also the overall range loss is greater than the average for terrestrial large carnivores. To assess the leopard's status, we compile 6,000 records at 2,500 locations from over 1,300 sources on its historic (post 1750) and current distribution. We map the species across Africa and Asia, delineating areas where the species is confirmed present, is possibly present, is possibly extinct or is almost certainly extinct. The leopard now occupies 25–37% of its historic range, but this obscures important differences between subspecies. Of the nine recognized subspecies, three (*P. p. pardus, fusca,* and *saxicolor*) account for 97% of the leopard's extant range while another three (*P. p. orientalis, nimr,* and *japonensis*) have each lost as much as 98% of their historic range. Isolation, small patch sizes, and few remaining patches further threaten the six subspecies that each have less than 100,000 km^2 of extant range. Approximately 17% of extant leopard range is protected, although some endangered subspecies have far less. We found that while leopard research was increasing, research effort was primarily on the subspecies with the most remaining range whereas subspecies that are most in need of urgent attention were neglected.

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Additional Information and Declarations can be found on page 20

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