

**ECOLOGY AND RESTORATION OF SUMATRAN TIGERS IN FOREST AND
PLANTATION LANDSCAPES**

Sunarto

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Marcella J. Kelly (Chair)
Michael R. Vaughan (Co-Chair)
Sybille Klenzendorf
Stephen P. Prisley
James D. Nichols
Dean F. Stauffer

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ABSTRACT

Tigers (*Panthera tigris* Linnaeus, 1758) are in danger of extinction. Their populations have declined from ~100,000 to only ~3,000 individuals in a century and their habitat has shrunk to less than 7% of the historic range. Of the five extant tiger subspecies, the Sumatran tiger (*Panthera tigris sumatrae* Pocock, 1929) is the most seriously threatened. Currently determined as Critically Endangered under IUCN criteria, the Sumatran tiger is likely to become extinct unless effective conservation measures are enacted. Threats to the tiger include habitat destruction, killing due to conflict with humans and livestock, and poaching for illegal wildlife trade.

Long-term survival of Sumatran tigers depends largely on the effectiveness of current conservation efforts in every tiger landscape. Successful conservation and management require accurate information on ecology of the species upon which decisions can be based. This study investigated basic ecological aspects of tigers and developed strategies for management and restoration to improve tiger viability in the Central Sumatra landscape. This landscape is comprised of natural forests and plantations managed for timber and agricultural commodities.

The first chapter assesses the variation in tiger abundance across forest types in Southern Riau, and over time in Tesso Nilo National Park, all in Central Sumatra. Using camera traps, my team and I systematically sampled five blocks representing three major forest types in the region: peat land, flat lowland, and hilly lowland. I found that tiger

abundance varied by forest type and through time. Excluding two sampling blocks where no tigers were photographed, the lowest tiger density was in peat land forest of Kerumutan, and the highest density was in the flat lowland forest of Tesso Nilo. Repeated sampling in the newly established Tesso Nilo National Park documented a trend of increasing tiger density (SE) from 0.90 (0.38) individuals/100 km² in 2005 to 1.70 (0.66) individuals/100 km² in 2008. Overall, tiger densities from this study were lower than most previous estimates from other parts of Sumatra. The trend of increasing tiger density in Tesso Nilo, however, suggests that the tiger population could be augmented by protection of habitats that were previously logged and severely disturbed.

The second chapter examines the occupancy and habitat-use of the tiger across the major landcover types (natural forest, acacia plantation, oilpalm plantation, rubber plantation, and mixed agriculture). I found that tigers used some plantation areas, although they significantly preferred forests over plantations. In all landcover types, sites with tiger detections had thicker understory cover than sites without tiger detection. Modeling tiger occupancy while recognizing that probability of detection is not always perfect, I found that tiger occupancy covaried positively and significantly with altitude and negatively, but not significantly, with distance-to-forest-cores. Probability of habitat use by tigers covaried positively and significantly with understory cover and altitude, and negatively and significantly with human settlement and landcover rank. The results suggested that with adjustments in plantation management, tigers could use or roam through plantations within the habitat mosaic provided that the plantations had adequate understory cover and low level of human activity. They also could use riparian forests (as

corridors) and smaller forest patches (as stepping stones) to travel between the main habitat patches across the forest and plantation landscape.

The third chapter investigates the ecological characteristics and possible inter-specific interactions among wild felids, including tigers and smaller cats, based on data collected using systematic camera trapping in combination with information on their natural history. I found that despite overlap in resource needs of the five felid species, each appears adapted to specific environmental conditions allowing coexistence with other felids. The five felid species used statistically different elevations, with the golden cat found to inhabit the highest elevation. Two-species occupancy models showed that all possible pairs of felid species tended to co-occur more frequently than expected by chance, indicating the tendency of every felid pair to maintain spatial coexistence rather than exclusion. Species of similar size or eating similar-sized prey generally tended to have low coefficients of temporal activity overlap, suggesting avoidance. Temporal avoidance is likely occurring in three pairs of felids, namely clouded leopards and golden cats, clouded leopards and marbled cats, and marbled cats and leopard cats. Based on the differences in morphological and ecological characteristics, and on patterns of spatial and temporal occurrence, I identified six possible mechanisms by which felids in Central Sumatra maintain coexistence. I discussed the implications of this study for management, focusing on how to balance diversity and abundance of felids.

The fourth chapter presents the tiger distribution models as a case study to illustrate the importance of accounting for uncertainty in species distribution mapping. I applied four modeling approaches, differing in how the response variable (tiger presence) is constructed and used in the models. I compared the performance and output of

different models based on the relative importance of variables, descriptive statistics of the predictions, cross comparison between models using an error matrix, and validation using tiger presence data collected from independent surveys. All models consistently identified forest area within the grid as one of the most important variables explaining tiger probability of occurrence. Three models identified altitude as another important factor. While the four models were consistent in predicting relatively high probability of tiger occurrence for high elevation forest areas such as Rimbang Baling and Bukit Tigapuluh, they generally had a lower level of agreement in predictions for low elevation areas, particularly the peat land in the northeastern part of the study area. Based on the results of cross evaluation of the predictions among models and validation with the independent data, I considered the occupancy model to be superior to the others. If data collection format permits, I advocate the use of occupancy instead of the other modeling techniques to develop predictive species distribution maps.

The last chapter constructs a strategy to restore the tiger population across the ecosystem of Central Sumatra through integration of knowledge on tiger ecology from previous chapters with consideration of the ecological conditions of the landscape in the region. The strategy combines existing knowledge of tiger conservation and regional ecosystem restoration. It recognizes the limitations and challenges of traditional nature protection and considers existing and new opportunities. Emerging opportunities and new mechanisms, such as direct and indirect economic incentives for nature conservation and restoration, are taken into account. These, coupled with increased awareness of the stakeholders, better policies and implementation of good governance, and the willingness

and know-how to maintain coexistence with wildlife among the local people, are expected to support and accelerate the recovery of tigers and their ecosystem.

for the tiger

and those who cannot live without wild things^{)}*

^{*)} inspired by Jeff Sikich, Aldo Leopold

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ATTRIBUTION

This section provides a brief description of the contribution by colleagues on the development of some chapters of this dissertation. I drafted each chapter of this dissertation basically as a stand-alone manuscript. All committee members contributed in the development of research proposal and the study design. Tiger Research Team from World Wildlife Fund Indonesia assisted in the collection and management of field data, including identification of tiger individuals. Dr. Marcella Kelly contributed in the analysis of capture-mark-recapture data (Chapter 1), reviewed and provided extensive comments and useful input on all drafts of the dissertation. Dr. James Nichols and Jim Hines assisted in the data analysis for density estimation (Chapter 1) and the occupancy models (Chapter 2). Dr. Dean Stauffer helped in the analysis on habitat selection (Chapter 2). K. Parakkasi contributed in the development of Chapter 3 and commented on the early draft manuscript of that chapter. Brian Gerber assisted in the analysis of circular data, and also showed how to use Program DENSITY, SPACECAP, and Program MARK for further analysis and discussion for tiger capture data. M.R. Darmaraj and C. Tredick read and provided comments on Chapter 1 and Chapter 2, respectively. R. Sugiyanti read some draft documents to check the grammar.

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GENERAL INTRODUCTION

Asia was once largely covered with natural areas in which the tiger (*Panthera tigris* Linnaeus, 1758) lived (Kitchener and Dugmore 2000). Until about a century ago, ~100,000 tigers still roamed in the variety of habitats on the continent (Global Tiger Recovery Program 2010a). Since then, the human world population, the majority of which lives in Asia, has doubled approximately every 23 years (www.prb.org), causing large portions of natural habitats to vanish, thus squeezing tigers into only about 7% of their historic range (Sanderson et al. 2006), and reducing their population to only ~3,000 individuals (Global Tiger Recovery Program 2010a). Recognized as endangered since 1975 (Morell 2007), the global tiger population and its habitat have steadily been declining (Chundawat et al. 2010) (Figure I.1).

Tigers have declined not only in the total number of individual and range of distribution, but also in terms of the number of subspecies. Three subspecies, Bali tigers (*P.t. balica*), Caspian tigers (*P.t. virgata*), and Javan tigers (*P.t. sondaica*), have respectively become extinct in the 1940s, 1970s, and 1980s (Seidensticker et al. 1999a) (Figure I.1). Meanwhile, the South China tiger (*P.t. amoyensis*), which was estimated to number between 20 and 30 individuals in 1998 (Seidensticker et al. 1999a), has recently been suspected to have gone extinct in the wild (Tilson et al. 2004).

Of the five extant tiger subspecies, the Sumatran tiger (*P. t. sumatrae* Pocock, 1929) is the most seriously threatened. Determined to be Critically Endangered under IUCN criteria (Linkie et al. 2008b, Chundawat et al. 2010), this subspecies is likely to be the next to go extinct. Although no systematic population monitoring has been conducted, evidence of forest cover loss (Forest Watch Indonesia and Global Forest Watch 2001, Achard et al. 2002, Holmes 2002,

Kinnaird et al. 2003b, Uryu et al. 2010), killings due to conflict with livestock or humans (Nyhus and Tilson 2004), and poaching and illegal wildlife trade (Linkie et al. 2003, Shepherd and Magnus 2004, Ng and Nemora 2007), have led scientists and conservationists to believe that the number of tigers in Sumatra has fallen steadily over the last few decades (Wibisono and Pusparini 2010).

Due to the deficiency of data, some potential tiger habitats in Central Sumatra were categorized by Wikramanayake et al. (1998) as ‘priority survey areas.’ With preliminary data on tiger presence becoming available during the course of this study, the status of these areas has been updated (Sanderson et al. 2006). The Central Sumatra Landscape was identified to contain a cluster of four global priority Tiger Conservation Landscapes (TCL; Sanderson et al. 2006, STF 2009) including Tesso Nilo in the center, Kuala Kampar-Kerumutan in the east, Bukit Tigapuluh in the south, and Rimbang-Baling in the west. Until my team and I conducted this study, these areas remained poorly understood in terms of tiger abundance and landscape-scale distribution, let alone the more complex ecological aspects of this species.

Whether or not Sumatran tigers will survive over the long-term depends largely on the effectiveness of current conservation efforts in every tiger landscape. Successful conservation and effective management of wildlife populations require accurate information about tiger ecology upon which decisions can be based. Despite its current critical status and the urgent need to prevent extinction, basic ecological aspects of the Sumatran tiger such as distribution, population status, and habitat use remain unknown, especially in the Central Sumatran landscapes.

The goals of this study were to investigate basic ecological aspects of tigers and develop strategies for the management and restoration of tigers in the landscape. Collaboratively

conducted with World Wildlife Fund, Indonesian Ministry of Forestry, and Virginia Tech, this study forms part of a larger and longer-term initiative to save tigers and other biological diversity, and at the same time promote ecological integrity and ecosystem function. In conjunction with this study, local students at MS and undergraduate levels are conducting supporting studies. Partial results of this study have been used to identify High Conservation Value Forests, develop a National Conservation Strategy Plan for Sumatran Tiger Conservation (Soehartono et al. 2007), contribute to the development of guidelines for Better Management Practices for acacia and oilpalm plantation industries to support tiger conservation, and develop final theses by students. This work has also been presented in a variety of conservation and scientific fora including through a poster at the Wild Felid Conference (Oxford University, 2007), and orally at the Graduate Student Symposium (Virginia Tech, 2010), the Society for Conservation Biology Conference (University of Alberta, 2010), the Organization of Fish and Wildlife Information Manager Annual Meeting (Kentucky, 2010), and the Training Course on the Economics of Tiger Conservation (Duke University, 2010).

This study involves direct field investigations and synthesis based on field data combined with existing knowledge of tiger ecology and the management/restoration of wildlife and habitats. The field investigations focused on three subject areas: first, the variation in tiger abundance within the natural forest areas in different forest blocks and over time in Tesso Nilo; second, the distribution, occupancy, and habitat use of tigers within and across different landcover types including forests and plantations; and third, the interactions among wild felids including tigers and smaller felid species. Each of these forms a separate paper in this dissertation that focuses on understanding the ecological aspects of the tiger. As part of the synthesis, I applied four different techniques to map tiger occurrence in Central Sumatra as a

case study to evaluate the uncertainty in predicting species distribution and to suggest best possible methods to use. Finally, based on the results of field investigations presented in the preceding chapters, in light of the available information pertinent to tiger ecology and wildlife and habitat management from other places, I propose a strategy to restore tigers and recover the ecosystems in the landscape.

STUDY AREA

Central Sumatra contains a cluster of four global priority Tiger Conservation Landscapes (TCL; Sanderson et al. 2006, STF 2009) constituting one of the last strongholds for Sumatran tiger conservation (Borner 1978). Tiger Conservation Landscapes in this area include Tesso Nilo in the center, Kuala Kampar-Kerumutan in the east, Bukit Tigapuluh in the south, and Rimbang-Baling in the west (Figure 1.2). This mega-landscape of Central Sumatra potentially is the key habitat for tigers in Sumatra due to its strategic position in maintaining connectivity with the other tiger landscapes. To the south from Rimbang-Baling lies the largest national park on the island which also is another global priority TCL, the Kerinci-Seblat Landscape. To the northwest, it connects to the clusters of protected areas in West Sumatra (Harau, Rimbo Panti) that can further be connected to Batang Gadis and other tiger habitats in Northern Sumatra. To the northeast, Kampar Peninsula can likely be connected with Giam Siak Kecil and Senepis, which cover the major peatland habitats on the island.

Not every global priority TCL in Central Sumatra contains areas with legal protection status. For example, in the Kampar-Kerumutan Landscape, protected areas of Kerumutan constitute only a relatively small portion of the total TCL area. Unlike in the lowland areas, the proportion of protected areas is higher, relatively, in the hilly areas of Bukit Tigapuluh TCL and Rimbang-Baling TCL. Unfortunately, however, the protected areas in these higher lands mostly cover areas with relatively steep terrain and exclude lower elevation areas and the flatter terrain in its periphery. With such conditions, the habitat areas likely supporting higher populations of large mammals such as elephants (*Elephas maximus*) and tigers are excluded from protection.

Initial surveys in Central Sumatra in 2005 revealed that while tiger sign were still widely found in the landscapes, rapid deforestation processes were taking place in the area. According to

Forest Watch Indonesia (FWI/GFW 2001), by the 1990s, Riau province contributed about 45% (2.6 million ha) to the total degraded forests on the whole island of Sumatra, mainly due to legal logging operations. An analysis of forest cover change for Riau Province from 1982 to 2007 documented 65% forest loss (Uryu et al. 2007; Figure I.3). Other analyses by Hardiono et al. (2003), Jarvie et al. (2003), and Setiabudi and Budiman (2005) revealed that, after being logged, the forests were converted mostly to plantations (mainly acacia, oil palm, rubber, and mixed agriculture). The loss of habitat not only brings direct consequences in lowering the number of tigers the landscapes can support (Sunarto 2007, Uryu et al. 2007), but also is believed to fuel conflicts with humans (Eyes on the Forest 2009). Riau has consistently stayed among the top three provinces in Sumatra with the highest rate of human-tiger conflict incidence (Nyhus and Tilson 2004, WWF 2008). Along with poaching and illegal wildlife trade, habitat loss and conflict constitute the ‘evil quartet’ leading to tiger extirpations from many areas.

This study investigates tiger ecology in the landscape using two major systematic survey methods, camera trapping and sign surveys on segmented transects, covering different areas within the landscape. Camera trapping, with the main goal to estimate tiger abundance/density, focused on natural forest areas in the landscape. Systematic sign surveys, also known as occupancy surveys, were conducted across different landcover types deemed to be used by tigers in the landscape, including forest and plantation areas.

There are four major forest blocks in the Central Sumatran Landscape where this study was conducted. They range from sea-level peat land of Kampar and Kerumutan blocks, to relatively flat forest in the lowland of Tesso Nilo, to hilly and higher land areas of Rimbang Baling and Peranap-Bukit Tigapuluh. Except for Kampar peninsula, which largely is not protected with firm status, the other forest blocks generally contain a relatively large portion of

conservation area in the form of wildlife reserves or national parks. These include Rimbang Baling Wildlife Reserve (RBWR), Tesso Nilo National Park (TNNP), Bukit Tigapuluh National Park (BTNP), and Kerumutan Wildlife Reserve (KRWR). Below are highlights of some characteristics of the five forest blocks in the landscape.

Kerumutan

A portion of this forest block known as Kerumutan Wildlife Reserve was established as a protected area on 6 June 1979. The ca. 120,000 ha reserve forms part of the larger Kerumutan peat swamp forest ecosystem. To the east from the reserve toward the coast of Central Sumatra rests some natural forest marked as concessions for acacia or oilpalm plantations. The elevation ranges from 1 to 5 m above sea level and precipitation averages 2,720 mm per year. More than 95% of the area contains peat of at least 4 m deep (Silalahi 2007).

Kerumutan, and also Kampar Peninsula, which represent the peatland forests, lie mostly below 50 m asl with extremely flat terrain. Large parts of these forests are inundated during the wet season (generally between November and April). Unlike the tropical rainforest in the mineral soils, peat swamp forests are generally known as an ecosystem low in species diversity and abundance (Whitten et al. 2000). These areas are mainly associated with the combination of limited availability of nutrients and extreme environmental variation.

The poor nutrient content results from the fact that most vegetation does not go through complete decomposition and, instead accumulates as peat, upon which only certain types of plants with special adaptations can grow. Meanwhile, these areas are mostly inundated during the rainy season with some tidal influence. Changes from dry to wet/inundation cause biotic changes equivalent to the change between summer and winter in temperate lands. One theory of

diversity suggests that areas with such drastic environmental variation tend to have lower species diversity compared to areas with more stable conditions (Dobzhansky 1950, Paine 1966).

Peat land is poor in nutrients and very acidic. As a consequence, it has limited primary productivity and requires special adaptation to support plants and animals (Whitten et al. 2000). Due to these limitations, the habitat generally is considered unable to support high abundances of terrestrial wildlife. Nevertheless, such an area has high conservation value because it is home to some unique communities of vegetation, fishes, and wildlife species.

For logistical reasons these areas were only sampled during the non-flooding season. When the sampling extended into the wet season, which happened in Kerumutan, some of the camera trap stations became inundated at the end of sampling.

Kampar Peninsula

To the north of Kerumutan, separated only by the Kampar River, the Kampar Peninsula also consists of deep peat land that still contains a vast amount of natural forest. Wikramanayake et al. (1998) recognized both Kerumutan and Kampar as Tiger Conservation Unit (TCU) # 150 and categorized it as TCU Level II, considered to “offer medium probability of persistence of a tiger population over the long term.” The Sumatran Tiger Conservation Program and Sumatran Tiger Trust (STCP&STT 2005) documented that the area likely contains a high density of tigers and their prey. Unlike Kerumutan, with a relatively large area already under legal protection, to date most of the area in Kampar Peninsula remains unprotected. The total forest cover in 2004 was ~425,000 ha, a decline of ~25% from 2001 (STCP&STT 2005). A rapid survey in Serapung, a portion of the Kampar Peninsula near the coastline, documented a relatively high detection rate of tigers and ungulates (STCP&STT 2005). Containing vegetation materials that are not fully decomposed, peat lands hold massive amounts of CO₂ that will be released to the atmosphere as

peat becomes dried or burned when forests are degraded or converted to other forms of landcover. Kampar Peninsula, as well as Kerumutan areas, therefore, possess global significance in driving climate change (Uryu et al. 2007). For that reason, environmental groups continue to advocate the protection of the area while pulp and paper and agricultural companies and farmers are converting the forest into plantations.

Tesso Nilo

The forest in Tesso Nilo shrunk rapidly in the past few decades. Covering an area of ~500,000 ha in the 1980s, the forests only covered ~200,000 ha in early 2000s. By the time this study was conducted, forest area measured only slightly over 100,000 ha. It has recently been described as a “an island in the ocean of plantations” (Glastra 2003). This forest complex was used as logging concessions operated by four different companies. Part of this area, (~38,576 ha), has been established as the first phase of Tesso Nilo National Park in 10 July 2004. The adjacent remaining forest to the northwest of the national park has been proposed to become the park’s extension. During the period of this study, the proposed extension area held a status quo (has obscure management status and unclear ownership status), but illegal activities were flourishing, mainly in the forms of illegal logging and encroachment of agriculture. In October 2009 the Ministry of Forestry partly approved the proposal and added 44,492 ha area as an extension of the existing national park.

In terms of floral diversity in a given sample plot, Tesso Nilo forest has been identified as the richest tropical dry lowland forest on earth (Gillison 2001). The forest block has high conservation value for elephants and tigers, among other species of conservation interest in Sumatra (Prawiradilaga et al. 2003, Departemen Kehutanan 2006). Tesso Nilo is considered to have the highest probability of survival for elephants among eight remaining habitat patches in

Riau (Desai 2007). The other areas have such high habitat loss and persistent human-elephant conflict, that elephant populations are considered doomed. Preliminary analysis also shows that Tesso Nilo holds the highest density of tigers compared to other forest blocks sampled in the region (Sunarto et al. 2007). However, the forests and wildlife in Tesso Nilo are threatened due to illegal logging and large-scale conversion to industrial plantations in the early 2000s (Holden 2002, Glastra 2003). The current threats have shifted from illegal logging to land claims followed by forest conversion to small scale agriculture and settlements.

Peranap

This area was established as a logging concession in 1993. By the time of this study, legal logging activity was no longer in operation. While parts of the ex-concession were already converted to agricultural and industrial plantations, the status of many other parts remained unclear and was disputed between local communities and companies. Conservation groups proposed that the area should be protected and integrated with the adjacent Bukit Tigapuluh National Park. The area represents the transition from flat lowland forest to the more hilly areas. When the sampling for this study was conducted, massive forest conversion to either acacia or oilpalm plantation was ongoing. Along with the Protection Forests in the neighboring area, this ex-logging concession is expected to serve as a potential wildlife corridor that provides habitat connectivity for wide-ranging wildlife living in Bukit Tigapuluh NP and Rimbang Baling WR. It connects to the larger forest block in Jambi Province. Just as for some forest blocks in Jambi, this forest area is also home to Orang Rimba, an indigenous nomadic forest dweller community of Malay people who subsist predominantly through hunting and gathering. In addition, there are also communities of Old Malay (Talang Mamak) tribal groups settled around the forest area (Franklin et al. 2004).

Rimbang Baling

The area is dominated by hills and submontane forests with slope ranging from 25%-100% (Hadi 2000). Rimbang Baling was established as wildlife reserve in 1982 with total area of ~136,000 ha (Kenedie et al. 2002). Although human disturbance from logging and settlement or farming activities took place in some areas mainly along the river banks within and outside of the reserve boundary, the reserve generally contains pristine forests. The forest of Rimbang Baling extends beyond the reserve boundary both within Riau Province as well as toward West Sumatra Province. During the field work, my team and I observed that illegal logging sporadically took place within the boundary and some of its interior. However, it was generally smaller in scale compared to illegal logging in the more flat and lower elevation in Peranap or Tesso Nilo. The reserve borders some industrial activities such as acacia plantations for pulp-and-paper, mining for coal, and oilpalm plantations.

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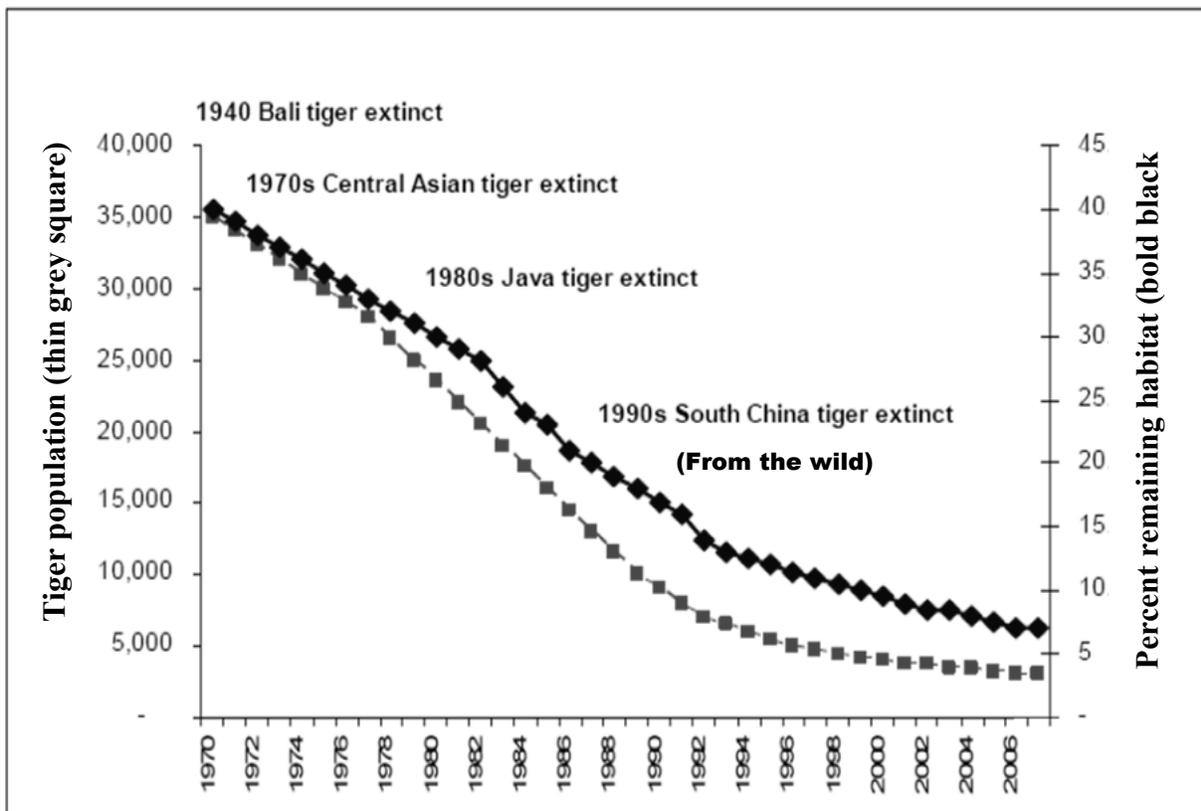


Figure I.1. Habitat loss, declining population, and subspecies extinction of tigers in Asia from 1970s to 2008 (Figure modified from Global Tiger Recovery Program 2010a).

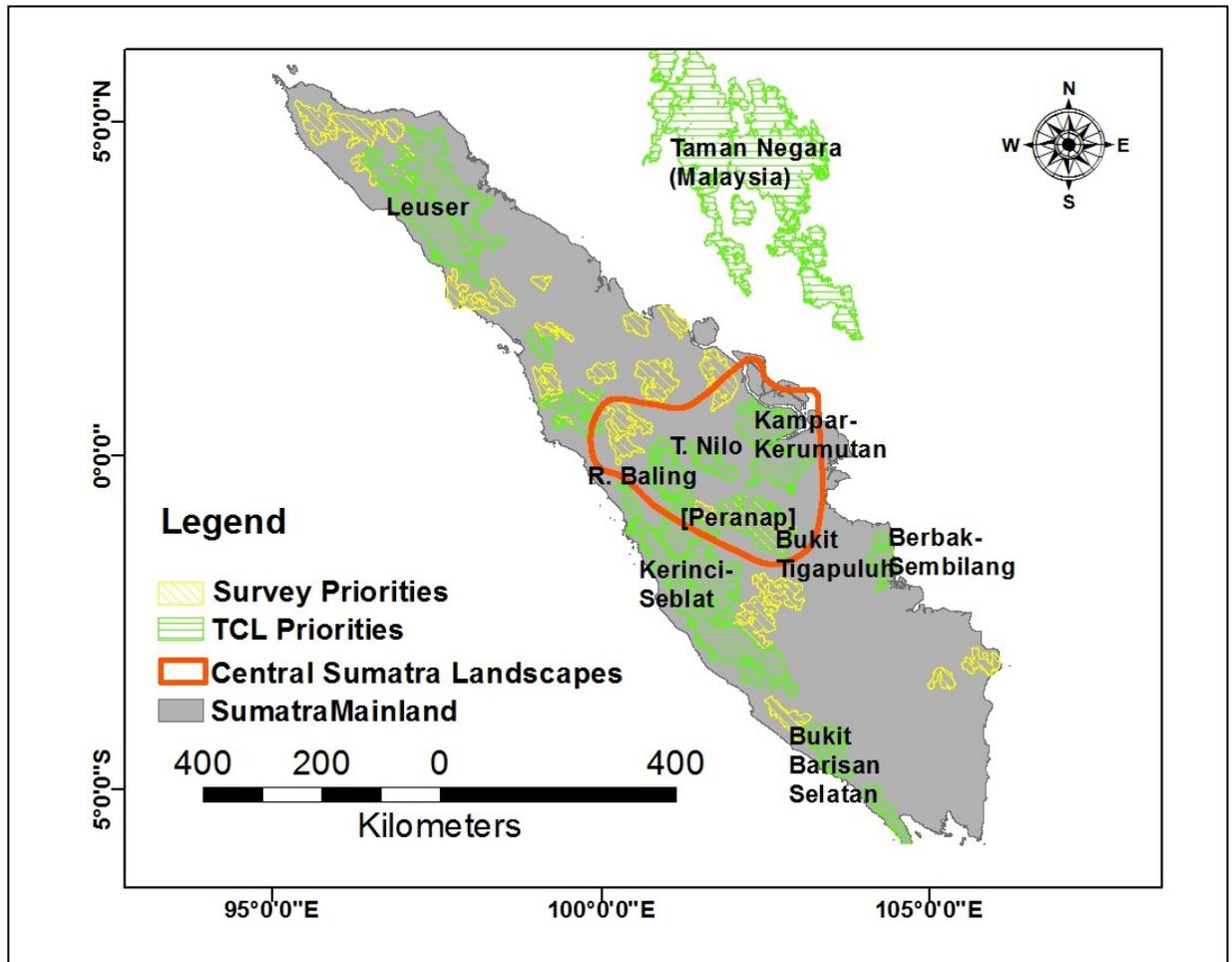


Figure I.2. Location of study area in Central Sumatra and Tiger Conservation Landscapes (TCL) within and around the study area.

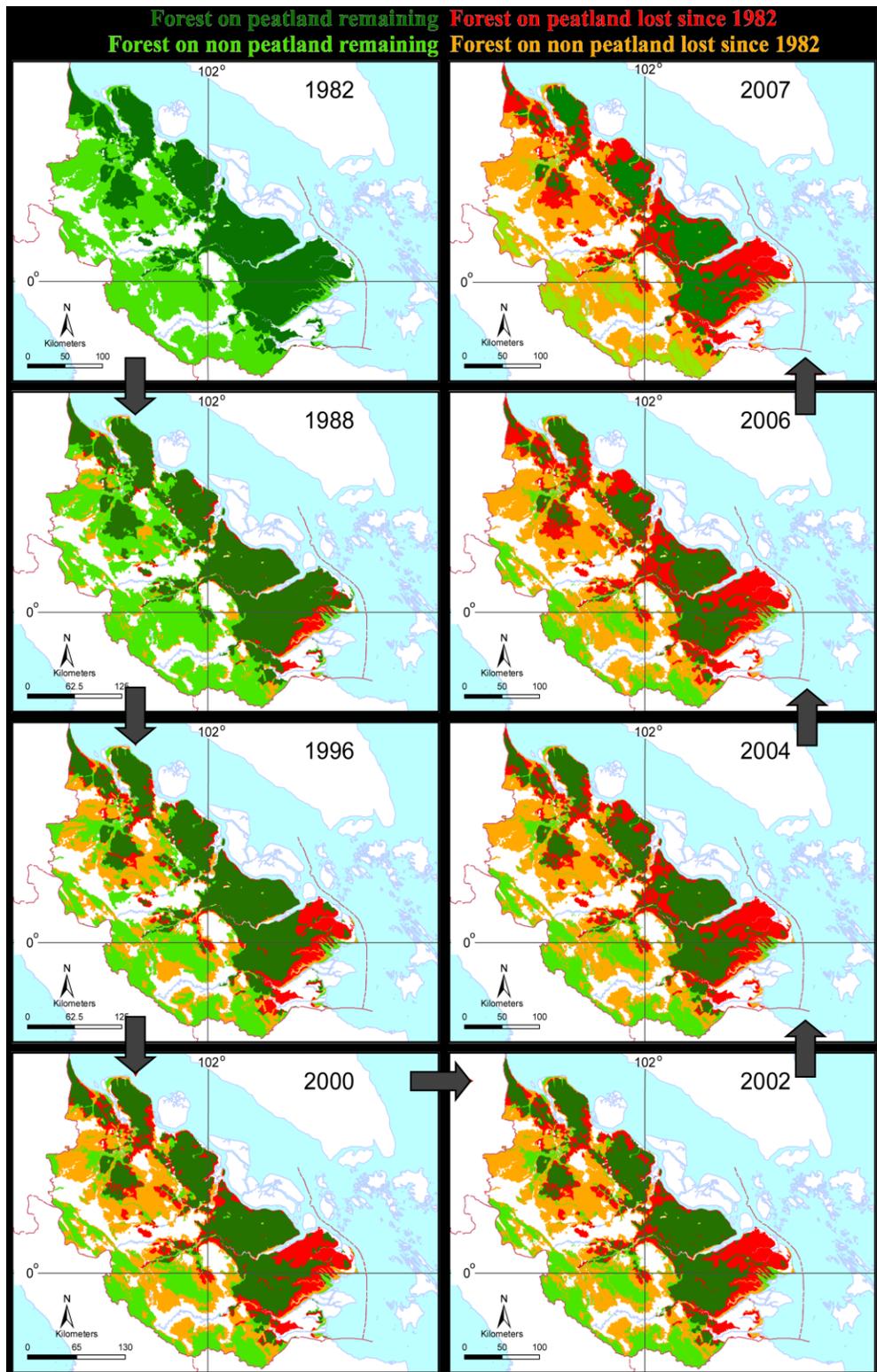


Figure I.3. Change in forest cover in Riau Province from 1982 to 2007 (From Uryu et al. 2007; - used with permission)

Chapter 1

Tigers on the equator: variation in abundance across forest types in southern Riau and over time in Tesso Nilo National Park, Central Sumatra

“*Why should large hunting animals always be so amazingly rare?*” Colinvaux, 1978

ABSTRACT

Although considered the most seriously threatened among the five extant tiger subspecies, information on the abundance of the Sumatran tiger is still lacking from many areas within its distributional range including Riau, the province guesstimated to hold the largest percentage of the total Sumatran tiger population in the wild. This study investigated the variation in tiger abundance across forest types in southern Riau Province, and over time in Tesso Nilo National Park, Central Sumatra. Using camera traps, my team and I systematically sampled five blocks representing three major forest types in the region: peat land, flat lowland, and hilly lowland. I estimated tiger abundance using closed population capture-mark-recapture models with Program CAPTURE and calculated densities on the effective sampled areas measured using data from trap locations of animals captured multiple times, and also using spatially explicit capture-recapture (SECR) implemented in Program DENSITY. Photographic rates were used to indicate prey activity. I explored the relationships between tiger density and prey activity, and other covariates from the sampling blocks including altitude and level of disturbance from human activity. Tiger abundance varied by forest type and through time. Excluding two sampling blocks where no tigers were photographed, based on Program CAPTURE, the lowest estimated tiger density (0.52 tigers/100km²; SE=0.27) was in peat land forest of Kerumutan and the highest density (1.7/100km²; SE=0.66) was documented in the flat lowland forest of Tesso Nilo. The repeated sampling in the newly established Tesso Nilo National Park documented a potential trend of increasing tiger density from 0.90 (0.38) in 2005 to 1.70 (0.66) individuals/100 km² in 2008. However, Program DENSITY resulted in lower estimates for all sampling blocks, by ~50% with no detectable trend over time. Overall, estimates of tiger density from this study were lower than most previous estimates from studies in other parts of Sumatra. I identified high levels of human activity as a critical factor potentially limiting tiger density even when requirements such as availability of vegetative cover and abundant prey were met. The establishment of Tesso Nilo National Park seemed to discourage and reduce some illegal human activity and thereby allowed previously disturbed habitat to recover. The stable or potentially increasing number of tigers in Tesso Nilo over time suggests that tiger population could be augmented by protection of areas that were previously logged and severely disturbed.

Keywords: anthropogenic disturbance, camera trapping, change in tiger density, crowding effect, habitat protection, *Panthera tigris sumatrae*, peatland forest, Sumatran tigers

INTRODUCTION

Determining population status is of utmost importance for the effective management of a species (Gilbert and Dodds 1987, Krausman 2002, Bolen and Robinson 2003). Among the basic information required to understand population status are abundance/density of the wildlife population, population trend, and population variation over spatial and temporal scales (Lancia et al. 1996, Williams et al. 2002). Additionally, the number of animals in a given area, relative change in abundance over time, and the combination of these factors are used to determine the conservation status of a species (IUCN 2001) and the actions required to conserve or manage the population (Nowell and Jackson 1996). Finally, understanding factors underpinning population size variations allows managers to identify possible interventions required to effectively manage populations.

Despite long recognition of the critical status of Sumatran tigers (Morell 2007, Linkie et al. 2008b), population status of this subspecies in the wild remains uncertain (Soehartono et al. 2007, Wibisono and Pusparini 2010). Meanwhile, variation in abundance across habitat types in Sumatra and changes in abundance over time remained poorly documented. Lack of information can be attributed to the rarity and elusiveness of this species, posing a challenge for estimating population size. Rigorously estimating tiger abundance requires a large investment of financial and human resources. In most situations, available resources simply do not exist. As a consequence, many areas within the range of the subspecies remain poorly surveyed or completely unsurveyed.

Until this study, Riau Province was no exception in terms of lack of information. Guesstimated to hold around 30% of the Sumatran tiger population in the late 1970s, Borner (1978) ranked Riau Province the first in Sumatra for the number of tigers potentially held. This estimate was based mainly on the total area potentially occupied by tigers. Riau Province harbors

not only hill and lowland forests, which are habitat types most commonly surveyed in previous studies in Sumatra, but also includes extensive peat land forests, which have never been studied for tiger population estimation.

The scenario based on Borner's (1978) original tiger population guesstimate unfortunately looked bleak as it was uncovered that a short while later rapid deforestation occurred in Sumatra (Forest Watch Indonesia and Global Forest Watch 2001, Uryu et al. 2010), particularly in Riau Province with an estimated deforestation rate of 65% over 25 years (forest cover declined from 78% in 1982 to 27% in 2007; Uryu et al. 2007). However, even with such conditions, this province still holds areas with high potential for tiger conservation and recovery (Wikramanayake et al. 1998, Sanderson et al. 2006), especially if further habitat destruction can be stopped (Uryu et al. 2007, Uryu et al. 2010) and degraded areas can be restored.

This study investigated the variation in tiger abundance across different forest types in the southern part of Riau Province and monitored changes in tiger abundance over time in the newly established Tesso Nilo National Park. I examined forests on sedimentary mineral soils and on the rarely surveyed peat alluvial lands to gain an understanding of spatial and temporal variation in tiger density, to identify factors that determine tiger numbers, and to explore management actions needed to effectively conserve and restore tigers in the landscape. Monitoring tiger population change through time in the newly established national park also allows us to evaluate the effectiveness of management interventions for tigers.

STUDY AREA

This study was conducted in several forest blocks scattered in the southern part of Riau Province in Central Sumatra (Figure 1.1; Table 1.1). Systematic photographic sampling using camera traps was concentrated in five sampling blocks covering three forest types including peat swamp

forest of Kampar Peninsula and Kerumutan (Figure 1.2), flat lowland forest of Tesso Nilo and Peranap, and the hilly lowland forest of Rimbang Baling. Except in Kampar Peninsula and Peranap, which were mostly not under legal protection, the remaining sampling blocks were protected as either wildlife reserves (Kerumutan and Rimbang Baling) or a National Park (Tesso Nilo). These forest blocks, interspersed with non-forested lands consisting mainly of acacia and oil palm plantations, form a multi-use landscape covering a total area of ~30,000 km². More detailed account of the major forest blocks in southern Riau where sampling was conducted is presented in Appendix 1.

METHODS

I estimated population densities of tigers using a capture-mark-recapture (CMR) approach with standardized camera trapping procedures. I used closed population models to estimate tiger population size in each sampling block (Figure 1.1). Each sampling block consisted of ~40, 2x2 km grid cells. My team and I established at least 20 camera stations at each sampling block, placing stations in every other 2x2 km grid cell.

Nichols and Karanth (2002b) suggest that CMR estimates for tigers could be conducted over 3 months without violating the closure assumption. Therefore, to avoid violation of the closure assumption, sampling was limited to 3 months.

To meet the assumption that no individuals in the sampling area had a zero probability of being 'captured' the team established a camera station in every other 2x2 km grid cell. This assured at least 3 pairs of cameras occurred in every tiger's home range, assuming a home range size of ~50 km² in Sumatra (Franklin et al. 1999). This gave us confidence in case some cameras failed or were stolen. Spreading the cameras evenly also ensured that animals within the sampled area had relatively similar capture probabilities (Nichols and Karanth 2002b).

The team placed cameras non randomly (Karanth et al. 2002b) in each pre-determined grid cell to optimize tiger captures (e.g., suitable habitat, tiger sign) while avoiding human disturbance/vandalism.

If a suitable places to install cameras could not be found within the pre-determined grid cell, the team sought a new location in a neighboring grid. To select which neighboring cells to place the camera, the team considered camera coverage with respect to tigers' possible home-ranges and other considerations mentioned above.

At each selected site, the team installed a pair of opposing cameras at knee height, preferably on a living tree, at ~ 2 to 3 meters from the trail where animals were likely to pass. Putting the cameras at a knee-height also allowed tiger cubs, potential prey animals, and other small carnivores to trigger the camera.

We recorded the film ID and camera numbers, GPS coordinates, altitude, and the grid alphanumeric code for the sites at which cameras were installed plus date and time of camera set up and personnel involved in deployment and checking. Each film and camera had a unique number to ensure easier and faster tracking. By numbering cameras, we also could track the performance of each individual camera and made adjustments when necessary. Due to logistical constraints, we could check and replace batteries and film only every 30 days.

Collected film was promptly developed and digitized, and organized photographs were entered into the camera trapping database. Using guides such as Payne et al. (1994), van Strien (1983), and Francis (2001), my team and I identified all mammals to species. Tiger individuals were distinguished based on their unique stripe patterns (Karanth 1995).

Mitigating vandalism

The initial study documented about 5% of cameras were stolen for every month of deployment (~ 2 cameras per 1000 trap nights), a high rate compared to other camera trap studies in Sumatra that documented <1 camera loss per 1000 trap night (Tarmizi/YLI, Y. Dinata/FFI-DICE, D. Priatna/ZSL, W. Novarino/Andalas University, H. T. Wibisono/WCS, Personal communications). To address this problem, we used the inexpensive DeerCam[®] 200/300, placed them in areas with the lowest human activity, attached persuasive notes, and secured them with steel cable and padlocks.

Data Analysis

Tiger density estimation

I applied two approaches in estimating tiger density. First, for comparison with the results from previous studies in Sumatra using the same approach, I used Program CAPTURE (Rexstad and Burnham 1992) to generate estimates of tiger abundance using the K-sample closed population CMR models based on camera trapping data (Nichols and Karanth 2002b).

To prepare the detection history data for Program CAPTURE, I collapsed every 10-days into one sampling occasion. This number was considered a good compromise between reducing zeros and retaining different detections. With ~3 months sampling period, this gave us nine or ten sampling occasions in the detection history. In CAPTURE, I used the Jackknife estimator for the heterogeneity model (M_h), which performed well and is considered the most robust of all models (Nichols and Karanth 2002b). When the only competing model was M_0 (assuming equal capture probability for all animals), I used the Model M_h which allows each individual to have different and unique detection probabilities (Otis et al. 1978).

I calculated the density of tigers by dividing the abundance estimate from CAPTURE by the area from which animals were sampled (Karanth and Nichols 1998, Nichols and Karanth

2002b). Since the animals detected in camera traps may have home range centers outside of the polygon drawn around traps, it is necessary to estimate the area effectively sampled. I estimated the area effectively sampled as the polygon with the outermost cameras as the boundaries, plus a buffer (i.e Minimum Convex Polygon – MCP; Freeman and Shapira 1975, Laver 2005) or by directly buffering each camera location individually and merging the buffers into a polygon (Kelly 2003, Silver et al. 2004, Dillon and Kelly 2008, Kolowski and Alonso 2010). In calculating the buffer for both approaches, I used $\frac{1}{2}$ mean maximum distance moved ($\frac{1}{2}$ MMDM) as the buffer around the polygon or the individual camera traps (Karanth and Nichols 1998).

Using the delta method (Nichols and Karanth 2002b), I calculated the variances for MMDM and boundary strip width to obtain 95% confidence intervals for tiger density. For sampling blocks that yield too few recaptures of tigers at more than one location, I borrowed recapture/movement distance data from the nearest blocks to obtain MMDM variance. I compared the difference between means of density estimates and their coefficients of variation (CV) resulting from the two approaches.

Second, I employed spatially explicit capture-mark-recapture (SECR) modeling techniques within maximum likelihood framework (Efford 2004, Efford et al. 2004), implemented in Program DENSITY 4.4 (Efford 2010). For this purpose, this method was preferred for practical reasons, including computer running time and flexibility in model development, over Bayesian approaches to hierarchical modeling (Royle and Young 2008, Royle et al. 2009a, Royle et al. 2009b) which can be implemented in R Package SPACECAP (Singh et al. 2010).

I developed capture history and trap activity input files for Program DENSITY with the same data for each sampling block and its respective sampling period (~3 months). Unlike

Program CAPTURE, I did not collapse detection history for Program DENSITY, and one occasion represents a 24-hour period of camera trapping. For every occasion, I marked each trap (camera station) as active (1) when at least one camera was in operational condition, or inactive (0) when no camera was working, and enabled incomplete trap layout in the input option in Program DENSITY. I used forest cover GIS layer from the same year of camera trapping (available from WWF; Uryu et al. 2007, Uryu et al. 2010), and added with 4 km buffer as the habitat mask. Four km has been used as the threshold of non-habitat that tigers would cross (Dinerstein et al. 1997, Sanderson et al. 2006) and I used this to account for additional habitats in the vicinity of forested land that tigers occasionally used (See Chapter 2).

Tiger density was estimated using conditional likelihood SECR with three different detection functions (half-normal, hazard rate, and negative exponential) assuming a Poisson distribution, all with constant model for intercept (i.e., the probability of capture when the trap and range centre coincide, $g_0[.]$) and spatial scale parameter ($\sigma[.]$). Covariates (such as time effect, response to capture, individual heterogeneity, or trap effect) were not used in any model due to limited number of samples (capture and recapture). The best model for each sampling block/period was selected based on Akaike Information Criteria (AIC; Akaike 1973) or, when applicable, the version corrected for small sample size (AICc) (Burnham and Anderson 1998).

Index of activity for humans and tiger's potential prey

As an indicator of disturbance, I assessed the level of human activity in each sampling block using the photographic rate of human and the level of vandalism (theft) to the cameras.

Using Chi-square goodness-of-fit statistics, I tested the differences between expected (under a null hypothesis of no difference) and observed numbers of independent pictures for primary prey species among sites, habitat types, and for Tesso Nilo, among years of sampling.

The expected numbers of independent pictures were calculated based on the proportion of effective trap nights for a given sampling block, forest type, or sampling period. I defined pictures as independent if: (a) animals were clearly different individuals, (b) when individuals were unidentifiable, the pictures were taken at least 30 minutes apart, and (c) where nonconsecutive pictures of individuals of the same species were obtained (O'Brien et al. 2003).

I defined effective trap nights as the number of nights multiplied by the number of camera stations minus any days where both cameras at a station malfunctioned. For paired cameras operated for the same 24-hour period in the same station, I considered this as one trap night. Appendix 2 describes the procedure in more detail.

For a descriptive comparison among sites or among sampling periods within the same site, I also calculated the photographic capture rates (PCR; O'Brien et al.(2003)). PCR for a given species was determined by calculating the number of independent pictures per 100 trap nights. The calculation of PCR focused on preferred prey of tigers which included medium to large ungulates (wild pigs, *Sus scrofa*; bearded pigs, *Sus barbatus*; muntjac, *Muntiacus muntjak*; and sambar deer, *Cervus unicolor*) and ground-dwelling primates (pig-tailed macaques, *Macaca nemestrina*)(Karanth and Sunquist 1995, Carbone et al. 1999, O'Brien et al. 2003, Sriyanto 2003, Kawanishi and Sunquist 2004).

Comparisons of tiger density estimates across Sumatra

I compiled existing published information on tiger abundance from other places in Sumatra for comparison with my results. For each study, I identified the location, the terrain, the habitat type, the year conducted, the estimates of tiger abundance, and the estimation method used. When available, I extracted the abundance estimate and its respective 95% confidence limits (CL). In

the case when CL is not given, I presented plausible lower and upper bounds of the estimate taking into account their approach to derive the estimate and description given in text.

Relationships between tiger density and selected covariates

I used various techniques to appraise possible relationship between tiger density estimates and selected covariates. The techniques included simple linear regression and fitting of trend lines through scatter plots. I used the tiger density estimated using Program CAPTURE as the dependent variable, and covariates such as altitude, size of core forest block, index of human activity, index of prey abundance as the predictor variables. I used observations for which values of both dependent and predictor variables were available. For areas where no tiger photograph was obtained but tiger presence positively documented based on other evidence, I assigned density as the midpoint between zero and the lowest density estimate from my study area. Due to limited observations, it was not considered appropriate to evaluate the changes in density by evaluating many predictor variables at the same time, for example by using multiple regression and model selection.

Statistical analyses were performed in Microsoft Excel[®] 2007, JMP[®] version 8, or Program R[®] version 2.10.1, unless noted otherwise.

RESULTS

From 10,690 effective trap nights, my team and I obtained a total of 174 independent tiger pictures (Figure 1.2; Tables 1.2 and 1.3) from which my team and I identified 18 unique individuals. For each sampling block, the total time of camera operation ranged from 1,132 effective trap nights (Kampar) to 1,868 (Kerumutan); while the number of active stations ranged from 18 (Kampar) to 25 (Tesso Nilo during 2008 sampling).

Overall, I obtained most samples, both in terms of number of tiger photographs and number of unique individuals, from Tesso Nilo. Unlike other sampling blocks that were sampled only once, Tesso Nilo was sampled in three different years: 2005, 2007, and 2008. There, the number of tiger photographs steadily increased, but the number of tiger individuals detected fluctuated from five to seven to six. Except for two tiger individuals (ID#07 & ID#08) that were captured (and recaptured) in three different years sampling in Tesso Nilo, other individuals were unique to each sampling period in a given forest block.

Despite the presence of tiger sign in every sampling block, the team failed to photograph tigers in Kampar and Peranap during our systematic camera trap samplings, as well as during the extended period of *ad hoc* sampling. In these two blocks, camera operations were largely disrupted by vandalism/theft of 16 cameras in Kampar and 3 in Peranap. In addition to losing camera units, we also documented relatively high human activity based on PCR (Table 1.2).

Tiger density estimates

Based on the model selection criteria in CAPTURE, model M_h was always the best or the next best model after model M_0 , with selection criteria ranging from 0.85 to 0.95 (Table 1.3).

Abundance was estimated using model M_h in Program CAPTURE in all cases. Closure tests indicated that the analysis did not statistically violate the closure assumption for any site ($P > 0.15$), except in one survey in Tesso Nilo in 2005 ($P = 0.04$).

This study documented MMDM of tigers in the overall study area, excluding zero, to be 10.21 km. On average, tigers moved the farthest in Kerumutan (MMDM= 14.36 km, $n=1$), followed by Tesso Nilo (MMDM=9.83 km, $n=10$), and Rimbang Baling (MMDM=9.79 km, $n=1$). However, maximum (21.68 km) and non-zero minimum (3.48 km) distances moved were both documented in Tesso Nilo.

The two approaches to estimating the area effectively sampled result in similar tiger densities, and their respective coefficient of variations. Overall, density estimates were slightly higher when I buffered individual camera stations (Mean=1.13 tigers/100km², SE=0.26, n=5) than when I buffered the MCP of the outer camera stations (Mean=1.02 tigers/100km², SE=0.20, n=5). However, buffering individual camera stations also resulted in slightly higher CVs (Mean=0.49 tigers/100km², SE=0.04, n=5) than buffering the MCP (Mean=0.47 tigers/100km², SE=0.03, n=5). To simplify further analysis and comparison, results presented will refer to the density estimates produced based on MCP buffering, unless noted otherwise.

Tiger density estimates varied both spatially across different forest types/blocks and temporally within the same site. Due to limited sampling, which resulted in extremely large confidence intervals, no single estimate was found to be significantly different from the others (Figure 1.3). Nevertheless, if I consider the density point estimates, there are some clear patterns that can be described. Point estimate of tiger density was higher in flat lowland forest of Tesso Nilo (mean = 1.2 individuals/100 km²) than in peat land of Kerumutan (0.5 individual/100 km², SE=0.27) or hilly lowland of Rimbang Baling (0.9 individual/100 km², SE=0.43).

For Kampar and Peranap, where we did not photograph tigers but observed their sign, I assumed that tiger density was lower than sites with the lowest estimates (Kerumutan). For the purpose of this examination, I assigned density of 0.3 individuals/100 km² for each of these areas. That number is about the midpoint between zero and 0.5 (the lowest density documented in Kerumutan). While I believe this is realistic, I have no way to assess the accuracy of the “guestimate.”

Estimates of density from SECR were consistently and substantially lower than those resulting from Program Capture ranging from 0.34 individual/100km² for Rimbang Baling to

0.87 individual/100km² for Tesso Nilo in 2007 (Tables 1.3&1.4; Figures 1.3a&b). Other notable differences were that, unlike results from Program CAPTURE, tiger density estimated using SECR remained relatively constant with no obvious trend. However, I still observed overall increase in estimated tiger density in Tesso Nilo from 2005 to either 2007 or 2008; and that estimates of tiger density from either Kerumutan or Rimbang Baling were still lower than those from any period of sampling in Tesso Nilo (Figure 1.3b).

Human activity

Despite several mitigation measures, this study still suffered relatively high vandalism causing a total loss of 24 camera units (~2.24 camera unit loss per 1000 effective trap night) during the systematic sampling. More cameras were lost during *ad hoc* camera trapping across the central Sumatra landscape. Only in two sampling blocks (Kerumutan and Rimbang Baling) did the team experience no loss of camera traps. We documented relatively high human activities in Kampar (PCR=3.3), Peranap (PCR=1.4), and, particularly during 2005 sampling, in Tesso Nilo (PCR=7.0) (Table 1.2). Although the difference was not statistically significant, I found much lower levels of estimated human activity in established protected areas (>3 years of establishment, mean PCR of human=0.45) than in non- or newly-protected areas (<1 year of establishment, mean PCR of human=3.9).

Activity of potential prey

Prey activity, by species or in combination as groups, were significantly different among sites (Chi-square, all $\chi^2 > 61$, df=4, all P<0.01) and among forest types (all $\chi^2 > 20$, df=2, all P<0.01) (Table 1.2). Within the same area of Tesso Nilo, however, I found a significant difference among years only for muntjac ($\chi^2 = 5.9$, df=2, P=0.05) and no significance for the combination of three ungulate species (wild pig, muntjak, and sambar; $\chi^2 = 4.23$, df=2, P=0.12); while other

species and combinations of ungulates and pig-tailed macaque varied significantly across the years (all $\chi^2 > 13$, $df=2$, all $P < 0.01$).

We documented the apparent absence of some species of ungulates in some sampling blocks. Sambars, for example, were photographed in only two sites, and one of those had extremely low numbers considering the effort. The sample in peat land forest resulted in zero sambar and zero or extremely low numbers of photographs of any ungulate (Table 1.2).

Relationships between tiger density and selected covariates

Linear regression analysis of tiger density revealed extremely low coefficients of determination ($R^2 < 0.1$) for covariates other than block size ($R^2 = 0.69$, $R^2_{adj} = 0.53$). Further examination found that second-order polynomial models fit much better (based on the R^2) compared to simple linear regressions for most of the relationships (Figure 1.4). Altitude (Figure 1.4a) and prey activities (Figure 1.4b) have similar relationships with tiger density, with positive relationships at the lower values of the independent variables, and negative relationships at the higher values. Relationships between tiger density and index of human activities (Figure 1.4c) or size of forest block (Figure 1.4d), were found to show the opposite pattern, with a negative relationship at the lower values and positive at the higher values of the independent variables.

Comparison of tiger abundances and overall tiger numbers

In most samplings, my study had estimated substantially lower tiger densities than the expected figure (Table 1.5; Figure 1.5). Seven tiger studies across regions in Sumatra that used standardized CMR technique have in average documented tiger density of 2.1 individuals/100 km^2 , with estimates ranged from 1.5 individuals/100 km^2 in submontane primary forest to 3.3 in lowland primary forest, both in Kerinci Seblat (Table 1.5).

DISCUSSION

Tiger abundance comparisons

Tiger density in central Sumatra varied by habitat, sampling block, and through time in the same area. However, due to small sample sizes and lower than expected capture rates, my results had low precision. This study had equal or larger effort in the number of trap nights and effective area sampled than those of many other studies, yet we obtained low numbers of tiger photos. For example, in India, Karanth et al. (2006) photographed 74 individuals in 5,725 trap nights, while we photographed only 18 unique individuals in 10,690 trap nights. On average Karanth et al. (2006) took 7.73 trap nights to photograph an individual while we took an average of 590 trap nights to photograph a tiger (76 times as much effort). In such cases of extremely low density, alternative monitoring methods, such as occupancy estimation, may satisfy management needs or scientific investigation more efficiently.

Based on previous studies in other places of Sumatra, I expected that tiger densities in this study area would be ≥ 1 tiger/100 km². However, compared to studies using similar standardized CMR techniques, this study had lower tiger densities than expected, often below 1 tiger/100 km² (Karanth and Nichols 1998, Kawanishi and Sunquist 2004, Karanth et al. 2006, Linkie et al. 2006, Rayan and Mohamad 2009), even compared to similar habitat. Using SECR techniques, estimates of tiger density in my study area were even lower by almost 50% compared to the estimates from Program CAPTURE. Although not necessarily always the case (as in Jaguar estimation in Belize, Kelly (Pers. Comm)), in many instances SECR methods have been shown to produce lower density estimates than Program Capture with (½MMDM) buffer strip methods (Tredick and Vaughan 2009, Sharma et al. 2010; Gerber et al, under review). Therefore, I suggest re-analyzing density estimates from other areas using SECR techniques to prevent

overly optimistic tiger population numbers in Sumatra, particularly for those estimates derived using conversion factor from photographic capture rate.

While differences between tiger densities in India and Sumatra have been recognized, variation in tiger density in the same habitat type across geographical extent in Sumatra has rarely been discussed. For example, in the lowland forest of Kerinci Seblat, Sumatra, the estimated tiger density was 3.3 individuals/100 km²; almost 3 times my highest density estimate of 1.2 individuals/100 km² in Tesso Nilo. Factors likely to influence the differences in tiger density between the two regions include protection status (on paper and in the field), disturbance level from human activities, hunting pressure, prey availability, and vegetative conditions.

Prey activity

While prey availability has been identified as the single most important factor to determine tiger abundance (Karanth et al. 2004), and that depletion of prey significantly influence tiger population viability (Karanth and Smith 1999), this study documented that photographic capture rate of prey *per se* was not a sufficient predictor of tiger density. Results from this study suggest a nonlinear and more complex relationship between tiger density and relative abundance of prey (Figure 1.4). High tiger densities were not always documented in places with high relative abundance of prey. For example, in Peranap, which had very low tiger density, we not only documented the highest relative abundance of prey animals, but also the most diverse prey assemblage. This area even included sambar deer, which were absent in most other places. Sambar has the highest body mass of any potential prey in the area and should be the most preferred among other available prey detected in the area (Carbone and Gittleman 2002).

Tigers were not detected in the camera traps in Peranap, but we found their pugmarks during camera placement. I believe that tiger activity was strongly limited by the high level of

human activity, causing the animals to flee from the sampling area and/or hinder detection in camera traps. Human use included villagers or migrants conducting various activities in the forest and the nomadic indigenous community conducting subsistence hunting and gathering. Meanwhile, Riau Province is not only known for major transit in illegal wildlife trade (Ng and Nemora 2007), but also one of the main sources of tiger body and parts (Osmantri/WWF antipoaching team leader, personal communication; Shepherd and Magnus 2004). Notorious players, including one local person that claimed to have killed more than 50 tigers (Abi 2010) live and operated in the Province; and unprotected areas such as Peranap can easily become the operational target for poachers.

Relatively high levels of prey activity documented in Peranap suggested that unlike tigers, prey animals were less sensitive to human activities. High relative abundance of prey in Peranap also could occur as a consequence of tiger scarcity or temporal absence.

Unlike Peranap, the failure to detect tigers in Kampar is likely related to the low abundance of tigers due to the combination of both low prey availability and high levels of human activity. Prey availability is very low in peat land forests, likely due to low primary productivity and high levels of plant defense mechanisms, repelling herbivory (Whitten et al. 2000). Most ungulates were lacking in the camera trap samples from both Kerumutan and Kampar. The loose and porous texture of peat makes it difficult to move through, especially for animals such as ungulates that have relatively high body mass and long pointed feet. Additionally, many of the areas were inundated during the rainy season, making movement and feeding challenging for terrestrial animals. With the ability to climb trees to move and forage, pig-tailed macaque do well in these areas, and could become the main prey available for tigers in these areas. Sign of sun bears (*Helarctos malayanus*) was also commonly detected in this area.

Sun bears are able to make use of the higher forest stratum to forage and travel, and could potentially be tiger prey (Sriyanto 2003).

Tiger abundance and possible determinants

The low capture rates and densities of tigers documented across the study area are likely related to many factors including habitat quality, prey availability, human activity, and size of forest block. High levels of human activity within and around each sampling block were expected because, during the last decade, Riau had the highest human population growth (~4%) among other provinces, not only within Sumatra, but throughout Indonesia (BAPPENAS 2005). Many people we met in the forest were migrants from other provinces whose activities included logging, hunting/trapping, or opening forests for plantations, typically targeting forests with disputed ownership status as indicated by lack of signs of active management or protection. During their operation from 2007 to early 2010, WWF anti-poaching team detected and confiscated 87 metal snares typically used for tigers and 265 nylon snares for other animals (Osmantri/WWF anti-poaching team leader, personal communication).

The fact that zero camera trap loss took place only in Kerumutan and Rimbang Baling (both of which were the only sampling blocks in the study areas legally protected for decades) suggests that long-term legal protection of these areas was recognized by local people and migrants, discouraging them from trespassing and committing illegal activities.

The impact of human activity on tiger abundance differed, however, depending on the size of forest block available for tigers. In relatively large forest blocks tigers presumably have more room to escape high levels of human activity. For example, we failed to detect tigers despite intensive surveys in Kampar (highest rate of camera vandalism and second highest human PCR; large core forest block=3060 km²), and in Peranap (second highest rate of camera

vandalism and third highest human PCR; core forest block=1860 km²). When high human activity took place in relatively small and isolated forest blocks such as Tesso Nilo (highest level of human activity in 2005 sampling; size of core forest block=860 km²), tigers remained detectable, perhaps because there was little or no room to escape detection. Comparing two sites with different levels of human activity in the northern part of Sumatra, Griffith and van Schaik (1993) documented significantly reduced activities of tigers and some other wildlife species in areas with higher level of human activities.

The fact that tigers were still using small areas like Tesso Nilo could be due to more preferred habitat conditions compared to the neighboring areas. Along with the drop in human activity in subsequent sampling, I documented a stable or potentially increasing trend in tiger density in this area. My observations in the field suggested that, in 2008, people appeared to halt activities when the National Park was established and actively managed. People then returned to the area, probably due to a combination of lack of livelihood alternatives and decreasing or stabilizing level of management activities/impacts.

Change in tiger density as a result of change in human activity is not unique to my study area, however, as an increase in tiger density also was documented in India following the removal of anthropogenic influences (Harihar et al. 2009). While reduction in the level of human activity likely contributed to the increase in tiger density in Tesso Nilo, the increase also could be related to the reduction of available habitat for tigers in the surrounding areas due to the intensive forest conversion activities outside the Park as illustrated by Uryu et al. (2007). Tiger density may have increased as a result of immigration rather than birth. An increase in animal density due to the loss of habitat in the surrounding areas could be a temporary phenomenon that may be followed by a stabilization at a lower density (Debinski and Holt 2000). Longer-term

tiger population monitoring such as using the Pollock's Robust Design (Nichols and Pollock 1990, Pollock et al. 1990) or reverse-time capture-recapture methods (Nichols et al. 2000) are needed to disentangle birth from immigration of individuals from neighboring forests, and special other analyses are needed to assess whether changes in density are due to the habitat improvement or other factors (e.g., van Horne 1983).

The relatively lower tiger density in Kerumutan and Rimbang Baling, compared to Tesso Nilo, was likely due to differences in habitat quality and prey availability. The peat land areas such as Kerumutan were not only poor in prey availability, but also extremely challenging for tigers or any large ground-dwelling animals to move. Meanwhile, in hilly areas such as Rimbang Baling, only a small portion of the area is useable due to difficult terrain.

My tiger density analysis was limited by the small number of samples. Larger sample size would allow us to draw stronger inferences regarding the relationships between tiger density and environmental variables. I recognize that ignoring the lower- and upper-bounds of the estimates might result in the failure to depict other important processes (Wiens 2002).

Graphical analysis using lower-order polynomials may result in ecological understanding that is useful for management (Guthery and Bingham 2007). Results of my examination suggest that there was no single variable that could explain the variation in tiger density without considering other factors. The variable of altitude in my study area appeared to be confounded with forest type. For the same forest types, I would expect to see a linear relationship with tiger density decreasing as elevation/slope increases. The relationship between tiger density and human activity seems to be conditional on whether or not tigers have more space to escape from areas with high level of human activity.

Management implications

The current endeavor of the global tiger conservation community (including the Global Tiger Initiative/The World Bank, Tigers Forever/Wildlife Conservation Society, and Tiger Initiative/WWF Network, among others) is to save the species by doubling or significantly increasing the global tiger population by the next decade (Global Tiger Recovery Program 2010a). Such a global vision seems optimistic, especially considering the massive deforestation that is still taking place in many areas including central Sumatra. For some areas, however, it is likely to increase tiger density if the limiting factors can be removed. This study suggests that, for the case of Central Sumatra, the most important factor to control is the high level of human illegal activity. Legal protection of an area, followed by intensive management, can discourage people from conducting illegal activities in tiger habitats.

Opportunities to legally protect or intensify the management of tiger habitats are still available. For example, the majority of the area in Kampar Peninsula, a large portion of the Kerumutan block, especially to the east from the wildlife reserve, the Peranap forest area, and forest in the vicinity of Rimbang Baling Wildlife Reserve are examples of tiger habitats that currently have little or no protection. However, without immediate action, these forest areas might not last due to the ubiquitous and rapid conversion activities. Therefore, efforts to conserve tigers in central Sumatra during this critical period should focus on legal protection and intensive management.

Traditional forms of protection such as national parks and wildlife reserves, have proven to be effective in reducing deforestation (Gaveau et al. 2007, Gaveau et al. 2009). There are also other alternatives available to improve tiger habitat while promoting local and national economic development. Such alternatives include forest protection to combat climate change involving carbon-trading (Reducing Emission from Deforestation and Forest Degradation, REDD++) that

include incentives for conservation of non-protected and protected area as well as biodiversity/species values, (UN 2008)) or establishment of ecosystem restoration such as in Hutan Harapan in Jambi Province (BirdLife 2008). Conversion of forest into acacia and oilpalm plantations largely stems from global market demands; therefore, the international community could share the responsibility and join forces with national and local communities to take more serious measures to save the tiger.

Conclusion

Sumatran tigers in central Sumatra live in much lower densities than those documented in many previous studies conducted in other areas of Sumatra. The findings suggest that the high levels of human activity is one of the key limiting factors preventing tigers from attaining higher density even when prey animals appear abundant. This was evident particularly in large forest blocks where tigers could still roam relatively free through, presumably, less disturbed areas.

The findings suggest that the total population of Sumatran tigers is likely lower than previously thought. For example, previous “guestimates” generally assumed that tiger density varied only by altitude, while the animal densities across forest types on the island were generally believed to be ≥ 1 individual/100 km². Many of my point estimates were < 1.0 and the resulting 95% confidence intervals of tiger density estimates above 1.0 included or were close to zero. This gives a strong indication that tigers might not do well in many areas even when the forest is seemingly relatively intact. More intensive monitoring and proactive management of tiger populations and their habitats are even more in demand if we are to avoid silent, local tiger extinctions.

This study presents a somewhat bleak picture. However, it casts some hope for tiger conservation in Sumatra as I documented an increasing trend in tiger density following the

establishment of Tesso Nilo as a national park, which presumably discouraged and reduced illegal human activities and allowed the disturbed habitat to recover.

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Table 1.1. Characteristics of the sampling blocks in Southern Riau Province, Central Sumatra.

	Kampar	Kerumutan	T.Nilo	Peranap	R.Baling
Geographic coordinates	0°17'N; 102°25'E	0° 4'S; 102°43'E	0° 8'S; 101°41'E	0°52'S; 101°57'E	0°22'S 101° 8'E
Mean elevation in meters (se)	20 (1.5)	33 (1.8)	71 (4.4)	132 (4.2)	219 (24.5)
Major soil type	Peat	Peat	Mineral	Mineral	Mineral
Composite criteria ^a	Alluvial and swamp	Alluvial and swamp	Sedimentary	Sedimentary	Metamorphic
Protection status (year established)	No-protection	Wildlife Reserve (1979)	National Park (2004)	No-protection	Wildlife Reserve (1982)
Ex-logging concession	Yes	No	Yes	Yes	Partly
Observed logging impact	High	Low	Very High	Medium	Low
Terrain	Flat	Flat	Generally flat	Flat to gentle hills	Gentle to steep hills
Wetness	Mostly inundated in rainy season	Mostly inundated in rainy season	Mostly Dry	Dry	Dry
Size of core forest block (km ²) ^b	3060	3790	860	1860	1680

^a Combination of geological, bioclimatic, geomorphologic and topographical maps as identified by Laumonier (1997).

^bObtained by measuring the forest area based on interpretation of Landsat images acquired in 2007 (done by WWF Indonesia GIS Team) after reducing with 3 km buffer, assuming edge effect.

Table 1.2. Systematic camera trapping effort and photographic capture rates of humans and main potential tiger prey in the sampling blocks in Central Sumatra, from 2005 to 2008.

	Kampar	Kerumutan	T.Nilo			Peranap	R.Baling
			2005	2007	2008		
Sampling period	20Jul07- 03Nov07	7Sep06- 17Dec06	31May05 -11Sep05	8Mar07- 18Jun07	12Apr08- 14Jul08	16Sep05- 29Dec05	19Apr06- 28Jul06
# Trap Stations	18 ^a	22	22	22	25	22	20
Effective Trap Nights	1,132	1,868	1,618	1,495	1,682	1,321	1,574
<i>Indicators of disturbance level during sampling</i>							
Camera loss	16	0	3	1	1	3	0
Human PCR*	3.3	0.1	7.0	0.3	0.4	1.4 ^b	1.0
<i>Prey activity (PCR* of main potential prey animals)</i>							
Sambar	0.0	0.0	0.0	0.0	0.1	2.3	0.0
Muntjac	0.0	0.0	4.0	5.6	4.1	14.6	3.8
Pigs	3.4	0.0	2.7	5.5	2.0	3.3	2.8
Pig-tailed macaques	10.5	8.7	9.7	3.3	7.7	10.3	14.4
Ungulates combined	3.4	0.0	6.7	11.1	6.1	20.2	6.6
Ungulates & pig-tailed macaques	14.0	8.7	16.4	14.4	13.8	30.5	21.0

^a Counted based on the position in 2x2 km grids. For the case of cameras being moved during sampling period due to security or other reasons, they are considered as one trap station if location is still in the same 2x2 grid. Total loss/failure of cameras in a given grid cell during sampling period renders the trap station uncounted. ^b Includes the presence of forest dweller indigenous people who live mainly on subsistence hunting and gathering; *Photographic Capture Rate.

Table 1.3. Tiger density (individuals/100km²) estimation summary for southern Riau Province, Central Sumatra.

	Kampar	Kerumutan	Tesso Nilo			Peranap	R.Baling
			2005	2007	2008		
# Tiger photos (0.5-hr independent)	0 ^a	14	38	40	75	0 ^a	7
Tiger PCR	NA	0.7	2.3	2.7	4.5	NA	0.4
# Tiger individuals detected	0 ^a	2	5	7	6	0 ^a	2
Area effectively sampled ^b (km ²)	559	582	779	617	470	431	354
Effective Trap Nights	1,132	1,868	1,618	1,495	1,682	1,321	1,574
MMDM ^c (sd)	NA	14.36 (NA)	11.37(5.92)	11.65(8.94)	7.31(3.97)	NA	9.79(NA)
Selection criteria under model M _h	NA	0.92	0.87	0.95	0.93	NA	0.85
Closure test z-value (P)	NA	-0.99 (0.16)	-1.75 (0.04)	-0.36 (0.36)	-0.89 (0.18)	NA	-0.30 (0.38)
Probability of capture (\hat{p}) ^d	NA	0.1667	0.2429	0.2429	0.2625	NA	0.1000
\hat{N} (se)	NA	3 (1.38)	7 (2.57)	7 (2.47)	8 (2.80)	NA	3 (1.36)
\hat{D} ^e (se)	NA	0.52 ^f (0.27)	0.89 (0.38)	1.13 (0.58)	1.70 (0.66)	NA	0.85 ^f (0.50)

^a) Tigers were confirmed to be present in the study area based on their sign (footprint and/or scat); ^b) Calculated based on Minimum Convex Polygon of outer camera points buffered with ½MMDM; for sampling blocks without tiger photographic captures, ½MMDM was borrowed from the nearest block; ^c) Mean maximum distance moved (in km), excluding zero distance moved animals; ^d) Based on data collapsed capture history with one occasion represents 10 trap days; ^e) Estimated density (individuals/100km²); ^f) Due to limited number of individuals photographed in this sampling block, to calculate density I borrowed data on tiger distance moved from the neighboring sampling blocks

Table 1.4. Model selection (ranked for each sampling session based on AIC) and estimates of tiger density (individuals/100km²) for Tesso Nilo (2005, 2007, 2008), Kerumutan (2006), and Rimbang Baling (2006) based on Spatially Explicit Capture Mark Recapture (SECR) with conditional Maximum Likelihood estimators in Program DENSSITY.

Detection Function	K	AIC	AICc	ΔAIC(c)	w _i	D(SE)	g ₀ (SE)	σ(SE)
Kerumutan 2006 (#Capture=6, #Animal=2, #Recapture=4)								
HazardRate	3	89.04	NA	0	0.5	0.41(0.29)	0.035(0.036)	1262.5(1172.7)
NegativeExponential	2	89.46	NA	0.42	0.4	0.34(0.24)	0.019(0.016)	2797.7(1534.9)
HalfNormal	2	90.86	NA	1.82	0.2	0.25(0.18)	0.006(0.005)	6025.6(2217.6)
Tesso Nilo 2005 (#Capture=27, #Animal=5, #Recapture=22)								
NegativeExponential	2	321.73	327.73	0	0.9	0.63(0.28)	0.060(0.025)	2227.6(475.9)
HalfNormal	2	326.59	332.59	4.86	0.1	0.59(0.26)	0.020(0.006)	4006.8(656.3)
HazardRate	3	321.79	345.79	18.06	0.0	0.59(0.26)	0.049(0.026)	2115.1(790.3)
Tesso Nilo 2007 (#Capture=26, #Animal=7, #Recapture=19)								
HalfNormal	2	317.07	320.07	0	1.0	0.87(0.33)	0.020(0.01)	5082.5(815.6)
HazardRate	3	321.38	329.38	9.31	0.0	0.84(0.32)	0.006(0.00)	12200(271.4)
NegativeExponential	2	341.49	344.49	24.42	0.0	0.72(0.27)	0.002(0.00)	NA
Tesso Nilo 2008 (#Capture=44, #Animal=6, #Recapture=38)								
HazardRate	3	441.53	453.53	0	0.7	0.8(0.33)	0.031(0.006)	8197.8(263.4)
HalfNormal	2	451.35	455.35	1.82	0.3	0.77(0.32)	0.063(0.019)	3907.7(399.2)
NegativeExponential	2	456.09	460.09	6.56	0.0	0.76(0.31)	0.210(0.120)	2212.3(333.4)
Rimbang Baling 2006 (#Capture=5, #Animal=2, Recapture=3)								
HalfNormal	2	74.19	NA	0	0.4	0.34(0.24)	0.006(0.005)	5630.7(4936.8)
NegativeExponential	2	74.26	NA	0.07	0.4	0.36(0.25)	0.012(0.015)	3716.9(5645.2)
HazardRate	3	75.72	NA	1.53	0.2	0.35(0.25)	0.004(0.003)	10093.0(332.1)

Notes: All model used consider no covariates (g₀[.].s[.]); Size of buffer used: 10,000 meter; AIC=Akaike Information Criteria, AICc=

AIC corrected for small sample; Dev=deviance; \hat{D} = estimated density (individuals/100km²); g₀= intercept (the probability of capture when the trap and range centre coincide); σ= sigma (a spatial scale parameter).

Table 1.5. Tiger density (individuals/100km²) estimates from various places in Sumatra in comparison to results from this study (in bold)

	Terrain	Forest Type	Protection Status	Density (ind/100 km ²)			Year of Study	Notes & Reference
				Median or average	Lower	Upper		
1.Leuser	Hill	Primary	NP	1.3	1.0	1.6	1992	1
2.Way Kambas	Flat Lowland	Secondary	NP	2.9	1.6	4.3	1995-1997	2
3.Jambi	Flat Lowland	Secondary	None	13.5	10	17	2001-2001	3
4.B. B. Selatan	Lowland Hill	Primary	NP	1.6	1.2	3.2	1998-1999	(CMR) ⁴
5.Kerinci Seblat	Lowland hill	Primary	NP	3.3	3.3	9.9	2001-2002	(CMR) ⁵
6.Kerinci Seblat	Hill	Primary	NP	2.0	2.0	4.1	2001-2002	(CMR) ⁵
7.Kerinci Seblat	Submontane	Primary	NP	1.5	1.5	4.0	2001-2002	(CMR) ⁵
8.Kerinci Seblat	Montane	Primary	NP	0.3	0.1	1.4	2001-2002	5
9.Batang Gadis	Hill	Primary	NP	1.8	1.8	6.4	2005-2006	(CMR) ⁶
10.Bungo	Hill	Secondary	None	3.0	2.5	5.0	2007	(CMR) ⁷
11.Ipuh	Hill	Secondary	None	1.55	1.3	2.9	2007	(CMR) ⁷
12.Tesso Nilo	Flat Lowland	Secondary	NP	1.2	0.2	2.3	2005-2008	(CMR)⁸
13.Peranap	Flat Lowland	Secondary	None	<0.5	NA	NA	2005	9
14.Kerumutan	Peatland	Primary	WR	0.5	0	1.0	2006	(CMR)
15.R. Baling	Lowland Hill	Primary	WR	0.9	0	1.7	2006	(CMR)
16.Kampar	Peatland	Secondary	None	<0.5	NA	NA	2007	9

Notes: (CMR) indicate study that use standardized CMR approach (Karanth and Nichols 2002) to estimate tiger density; ¹) Estimate in Gunung Leuser was done based on combination of camera trap total picture and GIS extrapolation. Density was derived from estimates of total population divided by total area(Griffiths 1994); ²) Value presented is the median between the low and high

estimates. Density in Way Kambas was estimated based on total number of resident individual photographed over 16 month of sampling and additional projected monthly average of non-resident individuals (Franklin et al. 1999); ³⁾ Maddox et al. (2007) estimated the density based on photographic capture rate using the conversion factor presented by Carbone et al. (2001); ⁴⁾ Estimate were made based on CMR with individuals identified based on pattern of left flank (O'Brien et al. 2003); ⁵⁾ (Linkie et al. 2006), estimate for montane forest was done based on encounter rate; ⁶⁾ (Wibisono et al. 2009); ⁷⁾ (Linkie et al. 2008a), ⁸⁾ Average values from three consecutive estimates using CMR (See Table 1.3); ⁹⁾ Despite confirmed to be presence, tiger were not photographed in camera traps during camera trap systematic sampling. Density is, therefore, assumed to be lower than site with the lowest density (Kerumutan). For the purpose of further synthesis, I assign density of 0.3 tiger/100 km² for these sites.

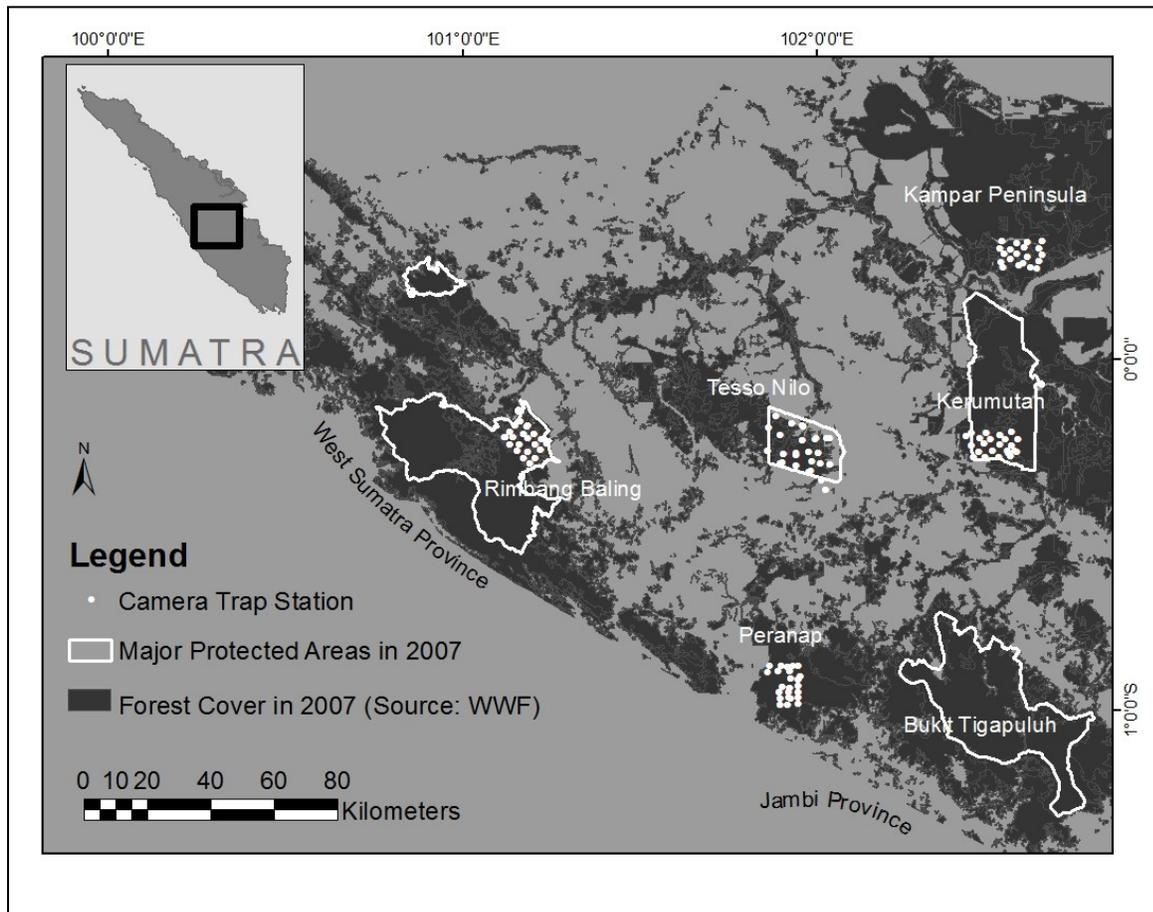


Figure 1.1. Map of the study area showing the Riau forest cover in 2007 with locations of systematic camera trapping grids in Central Sumatra.



Figure 1.2. An adult female tiger in inundated peat land of Kerumutan

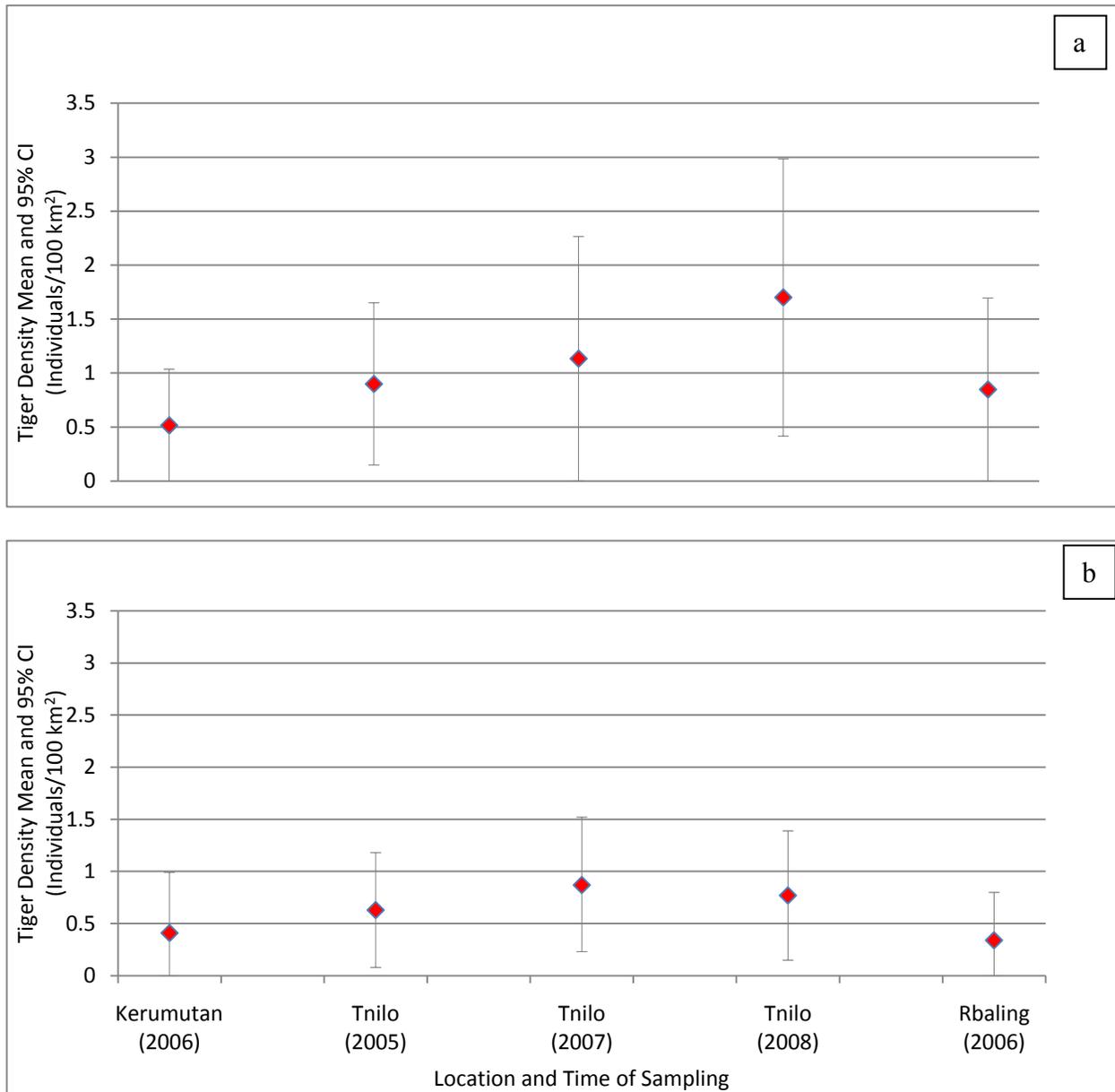
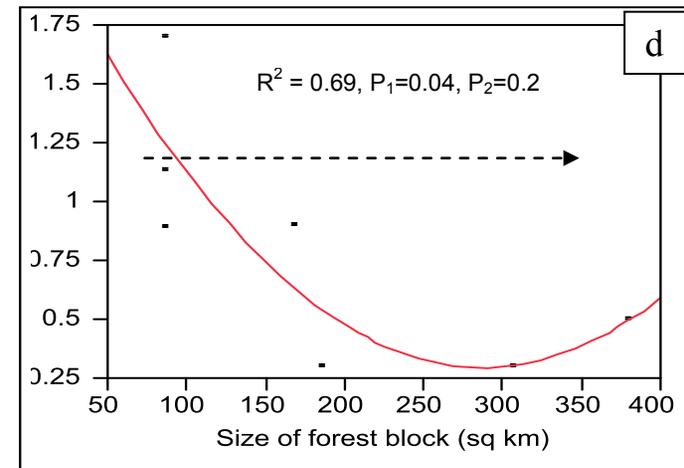
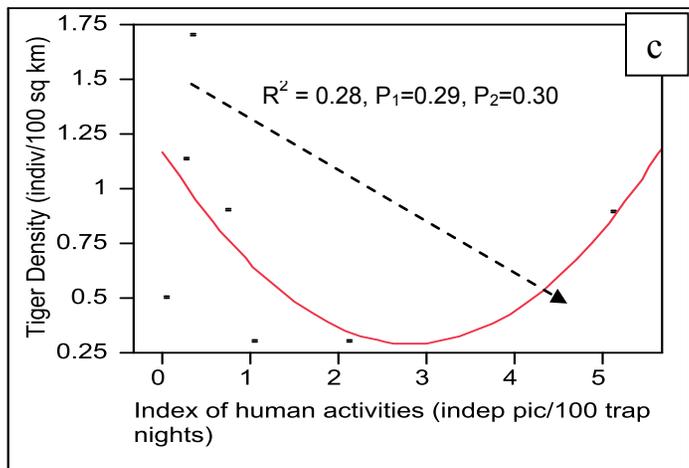
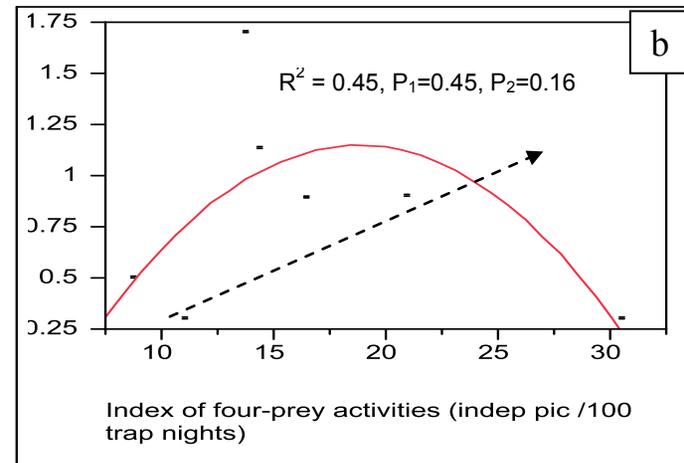
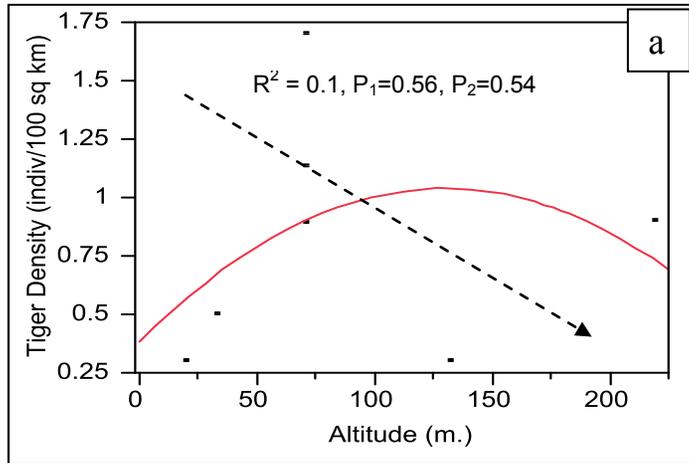


Figure 1.3. Tiger density (with 95% confidence limits) in five sampling sessions in three forest blocks of Central Sumatra where tigers were photographed, estimated based on a) Program Capture with effective sampling area determined using Minimum Convex Polygon (MCP) of camera traps with $\frac{1}{2}$ mean maximum distance moved ($\frac{1}{2}$ MMDM) buffer, and b) best model from conditional maximum likelihood Spatially Explicit Capture-Mark-Recapture (SECR) run in Program DENSITY



Notes: For areas where we did not photograph tigers, but positively documented tiger presence based on other evidence, we assigned density as the midpoint between zero and the lowest density estimate from our study area.

Figure 1.4. Relationships between various covariates [including a) altitude, b) prey activities, c) human activities, and d) size of forest block] and tiger density estimates (solid line) and a priori prediction (dashed line) in Central Sumatra.

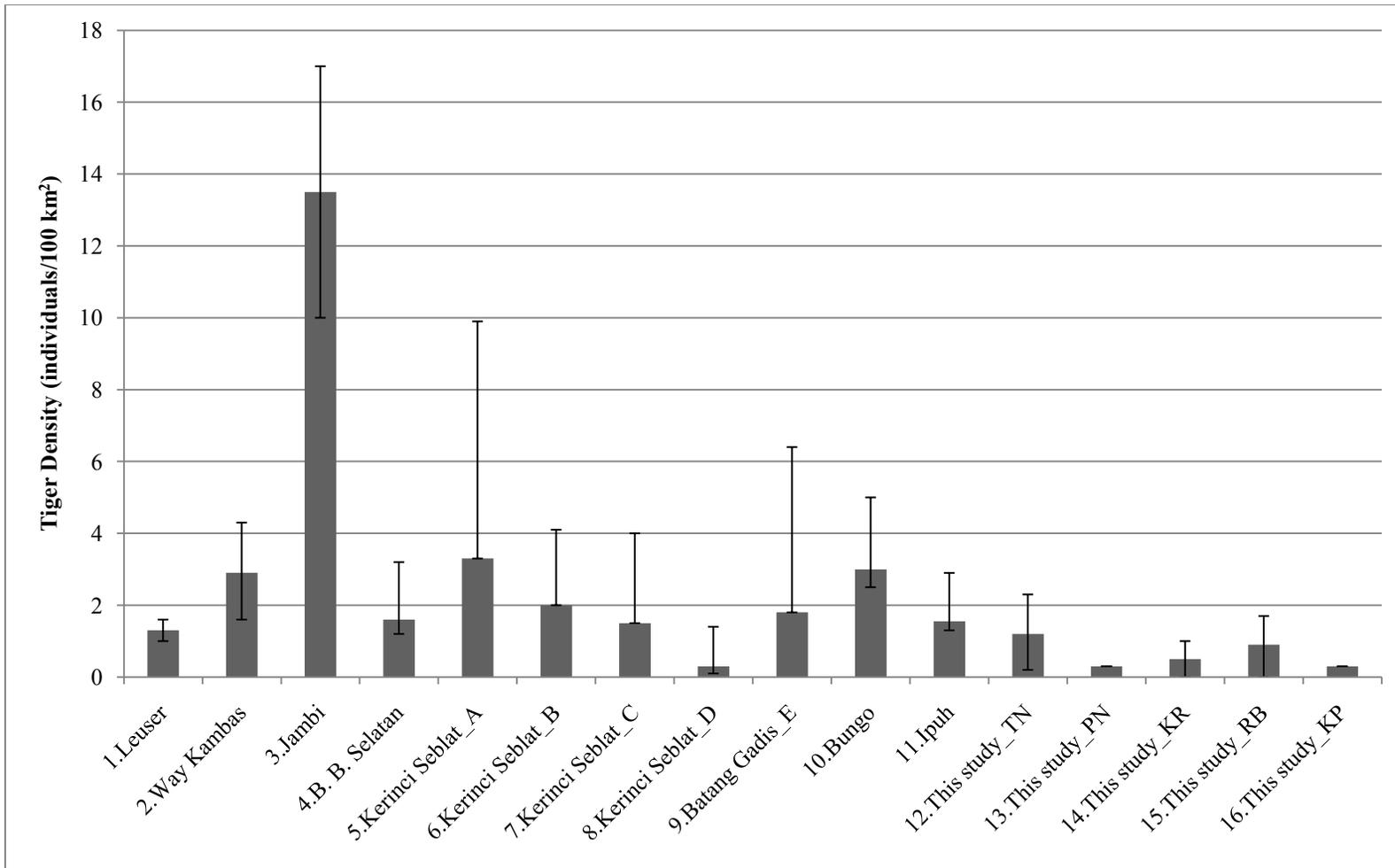


Figure 1.5. Tiger density estimates from various locations in Sumatra based on different studies (Detailed locations and study in Table 1.5).

Appendix 1.1 Detailed description of the major forest blocks surveyed in Central Sumatra.

1. Kerumutan

Established as a protected area on 6 June 1979, Kerumutan Wildlife Reserve is a peat swamp forest of ~120,000 ha forming part of the larger Kerumutan peat swamp forest ecosystem.

Elevation is ~1-5 m above sea level and climate is considered wet tropical. Peat and the drainage contain poor nutrient soils that are very acidic. As the consequence, there is limited primary productivity and the plants and animals require special adaptations to survive in such habitat (Whitten et al. 2000). Therefore, the habitat generally does not support an abundance of terrestrial wildlife. Nevertheless, such areas have high conservation value due to the unique assemblages of vegetation and aquatic animals. The area also has high significance for global climate due to the large amount of carbon stored as peat. More than 95% of the area contains peat of at least 4 m deep (Silalahi 2007). To the east of the reserve toward the eastern coast of Central Sumatra rests some natural forest most of which is marked as concession for acacia or oilpalm plantations.

2. Kampar Peninsula

To the north from Kerumutan, separated by the Kampar River, lies the Kampar Peninsula, which also consists of deep peat land and peat swamp forests. Wikramanayake et al. (1998) recognized both Kerumutan and Kampar as Tiger Conservation Unit (TCU) # 150 and categorized it as TCU Level II or considered to “offer medium probability of tiger persistence over the long term”. The Sumatran Tiger Conservation Program and Sumatran Tiger Trust (STCP&STT 2005) documented that the area likely contains high density of tigers and prey. Unlike Kerumutan that contains a relatively large area already under legal status of protection; most of the area in the Kampar Peninsula remains unprotected. The total forest cover is ~425,000 ha in 2004, a decline

of about 25% from the condition in 2001 (STCP&STT 2005). A rapid survey in Serapung, a portion of the Kampar Peninsula near the coastline, documented relatively high detection rate of tigers and ungulates (STCP&STT 2005). Containing vegetation materials that are not fully decomposed, peat lands hold a massive amount of CO₂ that will be released to the atmosphere as peat becomes dried or burned, which happens when forests are degraded or converted to other forms of landcover. The area, therefore, possesses global significance for climate change (Uryu et al. 2007). For that reason, environmental groups continue to advocate the protection of the area while timber companies and farmers were converting the forest into plantations.

3. Tesso Nilo Forest Complex

The forest in Tesso Nilo shrunk rapidly in the past few decades. Covering an area of about half a million hectares in the 1980s, the forests reduced to only ~200,000 ha in early 2000s. By the time this study was conducted, it measured only slightly over 100,000 ha, and was described as “an island in the ocean of plantations” (Glastra 2003). This forest complex was operated by four different companies and was almost entirely logging concessions. Part of this area, ~38,576 ha, was established as the first phase of Tesso Nilo National Park on 10 July 2004. The adjacent remaining forest to the northwest has been proposed to become Park’s extension. During this study the proposed extension area holds a status quo but illegal activities were flourishing mainly in the forms of logging and encroachment for agriculture. In 2009, 44,492 ha of the area was approved as the Park’s extension (Departemen Kehutanan 2009). In floral diversity, Tesso Nilo forest has been identified as the richest tropical dry lowland forest on earth (Gillison 2001). The forest block has high conservation value for elephants and tigers, among other species of conservation interest in Sumatra (Prawiradilaga et al. 2003, Departemen Kehutanan 2006). Tesso Nilo is the only one out of eight remaining habitat patches in Riau considered to have the highest

probability of survival for elephants (Desai 2007). Mostly due to habitat loss and persistent human-elephant conflicts, most of the other populations are considered doomed. Preliminary analysis shows that Tesso Nilo also contains relatively high abundance of tigers. However, the forests and wildlife in Tesso Nilo were threatened mostly due to illegal logging and large-scale conversion to industrial plantations in the early 2000 (Holden 2002, Glastra 2003). The current threats, as observed during this study, have shifted from illegal logging to land claims followed by forest conversion to small scale agriculture and settlements.

4. Peranap

Peranap area was established as a logging concession in 1993. By the time of this study, the company was no longer in operation. While parts of the ex-concession were already converted to agricultural and industrial plantations, many other parts remained disputed between local communities and companies. Conservation groups proposed that the area be protected and integrated with the adjacent Bukit Tigapuluh National Park. However, the companies were already in the process of converting the forest into acacia or oilpalm plantations. Natural forest in the area represents the transition from flat lowland forest to the more hilly areas. When sampling was conducted massive activities of forest conversion to either acacia or oilpalm plantations was ongoing. Along with the Protection Forests in the neighboring area, this ex-logging concession is expected to serve as a potential wildlife corridor providing habitat connectivity for wide-ranging wildlife living in Bukit Tigapuluh NP and Rimbang Baling Wildlife Reserve. This area connects to the larger forest block in neighboring Jambi Province. Just like some forest blocks in Jambi, this forest area is also home to Orang Rimba, an indigenous nomadic forest dwelling community of Malay people who subsist predominantly

through hunting and gathering. In addition, there are also communities of Old Malay (Talang Mamak) tribal groups settled around the forest area (Franklin et al. 2004).

5. Rimbang Baling

The area is dominated by hills and submontane forests with slope ranging from 25%-100% (Hadi 2000). Rimbang Baling was established as wildlife reserve in 1982 with total area of ~136,000 ha (Kenedie et al. 2002). Although human disturbance from logging and settlement or farming activities took place in some areas mainly along the river banks within and outside of the reserve boundary, the reserve generally contains pristine forests. The forest of Rimbang Baling extends beyond the reserve boundary both within Riau Province as well as toward West Sumatra Province. During the survey we observed illegal logging sporadically within the boundary and some of its interior. However, it was generally smaller in scale compared to that which took place in the more flat and lower elevation areas like Peranap or Tesso Nilo. The reserve borders some industrial activities, mainly acacia plantations for pulp-and-paper, mining for coal, and oilpalm plantations.

Appendix 1.2. Effective Trap Night calculation procedure

To determine photographic capture rate (PCR), from camera trapping, I need to standardize the number of photos by dividing by sampling effort, which can be represented as the number of trap days or trap nights.

When conducting survey, the team might leave the cameras for one month or more during each sampling in the field. However, this does not necessarily mean that the cameras are functional for that entire period of time. Calculating effective camera trap days or nights can often be challenging due to various conditions with the cameras. Cameras might fail due to battery failure, film shortage, animal damage, human vandalism, etc. Therefore, it is necessary to adjust the trap nights of camera by subtracting failures or nights when both cameras at a station are non-operational.

Generally, the team considered a camera trap to be effectively trapping if it is in good running condition (with sufficient batteries and film) and also the sensor and trigger are in good working order so that when a target animal is passing it is capable of taking a picture.

I define the effective trap night as the period between the time when the team leave the camera after installing the camera and film (hereafter, `DateTimeStart`) and the time when the camera stopped working effectively or was removed from the field (`DateTimeFinish`). In installing the camera and changing film, we always noted the time we left the camera when we set up new film and the time we arrive when we collect the film. While it is easy to determine the `DateTimeStart`, which is the time we leave the camera when we set up new film; determining the `DateTimeFinish` is a tricky task due to the fact that the date and time stamps also can fail. I used the following procedure (Figure 1.A1) to determine the time I consider the camera stopped working effectively (`DateTimeFinish`).

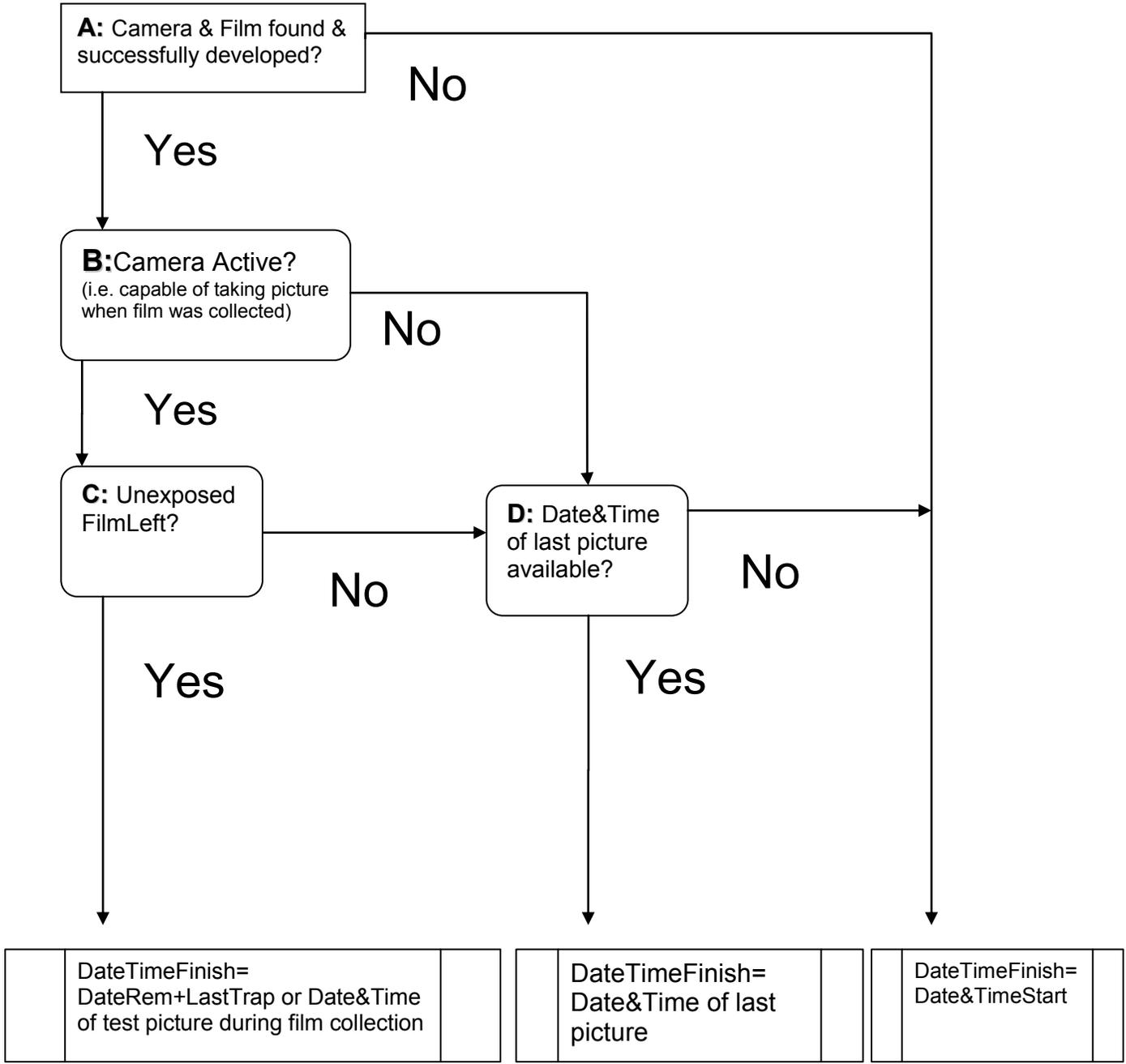


Figure 1.A1. Decision process to determine the time when the camera stop working effectively (DateTimeFinish) for camera trap operation

Chapter 2

Can tigers change their stripes? Multi-scale analysis of habitat characteristics, habitat selection, and occupancy of Sumatran tigers in forest and plantation landscapes

ABSTRACT

Tigers (*Panthera tigris*) in Sumatra are generally known as forest-dependent animals. With landscape change involving large-scale conversion of forests into plantations, however, it is crucial to understand to what extent these animals use these modified habitats. Such understanding is important for restoring this Critically Endangered subspecies. I investigated habitat-use and occupancy of tigers across major landcover types (natural forest, acacia plantation, oilpalm plantation, rubber plantation, mixed agriculture, and coconut plantation) in southern Riau Province, central Sumatra. My team and I conducted systematic detection, non-detection sign surveys in 47, 17x17 km grid cells. Within each cell, we surveyed an average of 40, 1-km transects and recorded tiger detections and habitat variables in 100m segments. In total we sampled 1,857 km. I found that tigers used some plantation areas, but significantly preferred forest (Habitat Selection Index, $\hat{w}[se]=1.4 [0.15]$) over plantations ($\hat{w}[se]=0.54[0.19]$). Tigers used plantations of acacia ($\hat{w}[se]=0.69[0.20]$), oilpalm ($\hat{w}[se]=0.15[0.11]$), and rubber ($\hat{w}[se]=0.09[0.09]$) far less than their availability. My team and I did not detect tigers in mixed agriculture or coconut plantations, likely due to their small size and distance and dissimilarities from forest landcover. In all landcover types, sites where tigers were detected had thicker understory cover than sites without tiger detections. Within forest areas, there were no significant differences in canopy or sub-canopy cover, but understory cover was significantly higher in sites where tigers were detected. Acacia sites with tiger detections had significantly older plants, taller trees, higher plant diversity, more leaf litter, less intensive plant husbandry, and significantly lower levels of human activity. I found that tiger probability of occupancy covaried positively and significantly with altitude, and negatively, but not significantly with distance-to-forest-centroids. Probability of habitat use by tigers covaried positively and significantly with understory cover and altitude, and negatively and significantly with human settlement and landcover rank. Within forest areas tigers significantly preferred sites that were farther from water and avoided sites with high human disturbance especially in the forms of encroachment and settlement. Tigers were significantly more likely to be detected in sites with steeper slopes. Within acacia plantations tigers significantly preferred sites that were closer to water and avoided sites with higher levels of logging activity. Tigers had a tendency to use older plantations for acacia and younger for oilpalm, both of which had higher plant diversity, and particularly for acacia, relatively lower levels of human activity. These results suggest that with adjustments in plantation management, tigers could use mosaics of plantations that had adequate understory cover with low levels of human activity (as additional roaming zones), riparian forests (as corridors) and smaller forest patches (as stepping stones) to travel between the main forest habitat patches. This study provides crucial information relevant for restoring the tiger population in forest and plantation landscapes through improvement in habitat extent, quality, and connectivity.

Keywords: carnivore restoration, habitat corridor, landscape connectivity, landscape restoration, plantation mosaics, tiger ecology, tiger habitat

INTRODUCTION

Although tigers (*Panthera tigris*) globally inhabit a variety of habitat types and are able to adapt to wide ranges of environmental conditions (Sunquist et al. 1999), in Sumatra they are generally believed to live only in natural forest areas. As such, forest conversion has typically been equated to absolute population extermination. Estimates of tiger populations, including projections of decline, have primarily also been derived from the extent of, or changes in, natural forest areas. In Sumatra, natural forests have largely been converted to forestry and agricultural types of plantations. Anecdotal information indicates, however, that such plantation areas are not totally useless for tigers. With recent and future changes in Sumatran landscapes that involve large-scale conversion of forests into plantations, it is crucial to understand whether existing plantation areas are useable by tigers. Furthermore, if tiger populations are to be recovered, it is also important to understand how habitat conditions within forests and plantations can be improved.

Habitat loss has widely been recognized as the main threat to Sumatran tigers (e.g., Linkie et al. 2008b). However, the use of habitats by tigers within, and especially outside of, natural forests has barely been studied. Previous studies of Sumatran tigers have largely focused on population estimation in pristine forests and/or within protected areas (Franklin et al. 1999, O'Brien et al. 2003, Wibisono et al. 2009). Only recently have some investigators begun to assess the value of non-pristine forests as tiger habitat (Linkie et al. 2008a). Except for Maddox et al. (2007), which included investigation of tigers in a non-cultivated conservation area within an oilpalm concession, there is no other study conducted in Sumatra examining use of non-forest areas by tigers. To my knowledge, this is the first study to systematically investigate and compare the use of habitats by Sumatran tigers in different landcover types within a multi-use

landscape. My investigation focused on Riau Province in central Sumatra, considered by Borner (1978) as the stronghold for Sumatran tiger conservation.

Distribution and habitat models

Distribution and habitat requirements of animals are key elements in ecology and basic prerequisites for effective wildlife management (Scott et al. 2002, Sinclair and Fryxell 2006). It also is important to construct reliable predictive models of animal occurrence based on solid understanding of the relationships between animals and habitat. Models that can accurately predict the probability of animal occurrence across an area of interest are urgently needed for wildlife management, but constructing such models for rare, elusive, and highly mobile species such as the Sumatran tiger is a demanding task. Due to data limitations, the distribution of tigers is often broadly mapped simply based on general knowledge and expert opinion regarding perceived potential habitats.

Understanding patterns of animal distribution requires consideration of the scale appropriate to address wildlife conservation needs (Osborne et al. 2001, Karanth et al. 2002a, Scott et al. 2002). That is because habitat selection, one of determining factors in animal distribution, takes place at variety of spatial and temporal scales (Johnson 1980, Miquelle et al. 1999, Morrison et al. 2006). While broad-scale tiger distribution maps such as the Tiger Conservation Unit (Wikramanayake et al. 1998) or the updated version, Tiger Conservation Landscapes (Sanderson et al. 2006), have been useful to direct conservation strategies at the global level, they are somewhat limited when it comes to local or regional landscape-level management purposes. Therefore, distribution models should consider aspects such as the appropriate scale (spatial and temporal), the predictive ability, and a rigorous assessment of uncertainty.

There are many approaches to creating predictive models of occupancy, occurrence, or distribution of a species (James and McCulloch 2002). Species distribution modeling usually consists of two steps: species-environment relationship analysis and extrapolation of the first step to larger areas (Corsi et al. 2000). Given the limited resources available to conduct field surveys in vast areas, the ability to accurately predict the probability of species' occurrence in a given area would contribute significantly to regional mapping (Osborne et al. 2001). With factors determining animal distribution identified for a certain area, one may predict the probability of the species occurrence, or identify potential habitat, across a larger region. Cayuela et al. (2009) provide a nice review of the most commonly used techniques in species distribution modeling.

A non-detection, however, is not necessarily a true absence and can give false information regarding true species distribution. An approach known as occupancy modeling (MacKenzie et al. 2002, Nichols and Karanth 2002a, MacKenzie et al. 2003, MacKenzie 2005) incorporates the probability of detection into the estimation procedure, recognizing that it is not always 1.0 (MacKenzie and Kendall 2002). This provides a more accurate depiction of animal distribution without the need to assume that all animals present in the surveyed area are detected (Nichols and Karanth 2002a). Application of such a technique has been done for some groups of animals including tigers in Kerinci-Seblat (Linkie et al. 2006) and the large mammal community in India (Karanth et al. 2009). By incorporating covariates into the models it is possible to describe the geographic range and habitat characteristics of the species of interest in the surveyed area (Gaston and Blackburn 1996, MacKenzie et al. 2004b), and also predict the probability of occupancy for, occurrence in, or use of, other sites not surveyed.

Recognizing that multiple-scale processes affect tiger distribution, and that analysis conducted at one single scale may be misleading (Maurer 2002), I developed models depicting

tigers and habitat relationships at multiple scales. In addition to estimating the probability of occupancy by tigers at the landscape-scale based on sampling conducted in 17x17 km grid cells, I also investigated the use, selection and characteristics of tiger habitats within forest and plantations based on sampling at 100-m segments along 1-km transects. My goals were: 1) to investigate factors affecting tiger probability of occupancy, 2) to construct a spatially-explicit species occurrence predictive model for the forest and plantation landscape in Central Sumatra; and 3) to describe habitat characteristics, and evaluate the use and selection by tigers between and within different landcover types.

STUDY AREA

This study was conducted in central Sumatra, covering the southern part of the Riau Province and small portions of Jambi and West Sumatra provinces (Figure 2.1). The initial survey in this mega-landscape found that Sumatran tigers were distributed in major protected areas including Tesso Nilo National Park, Bukit Tigapuluh National Park, Rimbang Baling Wildlife Reserve, and Kerumutan Wildlife Reserve and in forests outside of those protected areas (Chapter 1). Prior to this survey, tiger presence in plantation areas such as acacia, oilpalm, and rubber were limited to some anecdotal reports and had never been systematically documented.

The land cover is a mosaic of protected areas, towns and other human settlements, plantations (mainly acacia and oilpalm), mining, and secondary forests (Setiabudi and Budiman 2005, Uryu et al. 2007). While a relatively large portion of hilly, higher elevation forests are protected, this is not the case with lower elevation areas that include peat-swamp and mineral-soil forests. Examples of unprotected forests include those in Kampar Peninsula, those in the eastern part of the Kerumutan landscape, the north-western part of the Bukit Tigapuluh

landscape, and some areas just outside of Rimbang Baling Wildlife Reserve. A more detailed account of the study area is presented in Appendix 1.1 (Chapter 1).

METHODS

I used multiple approaches to describe, model, and predict occupancy and habitat use by tigers. First, to evaluate the relative importance of different landcover types within the landscape, I calculated the habitat selection ratio (\hat{w}), also known as resource selection (probability) function (RSPF) using the approach presented by Manly et al.(2002). Second, to explore the influence of different landscape covariates on the tiger's probability of occupancy at the landscape-scale, I used occupancy modeling techniques (MacKenzie et al. 2002, Nichols and Karanth 2002a, MacKenzie et al. 2003, MacKenzie 2005). Results from this modeling process were then used to develop spatially-explicit models depicting the tiger's probability of occurrence across the landscape. Third, I also used occupancy modeling techniques to investigate the influence of landscape/environmental/habitat variables on the use of habitat by tigers in forest and plantation areas at the landscape- and finer-scales.

I designed sampling in such a way that allowed me to analyze the resulting data for both occupancy estimation and assessment of habitat use/selection. Occupancy estimates depict the tiger's selection of a home-range within the landscape; while habitat use models represent selection of habitat within the home-range. These, respectively, are equivalent to second and third orders of habitat selection based on terms used by Johnson (1980). The survey covered all landcover types deemed potentially useable by tigers in the landscape. Following a common protocol proposed by Karanth et al. (2008), and scientists from other organizations working on large mammal research across the island of Sumatra, I used a standardized grid size of 17x17 km to represent each site with sampling occasions represented by 1-km transects within the grid

cells. The grid cell size was selected mainly because it approximated the home-range size of a tiger in a low density area (Griffiths 1994, Franklin et al. 1999). Occupancy therefore is more appropriately determined at the grid cell size whereas habitat use is determined when the grid cell size is smaller than the animal's home-range. Unlike other investigators who surveyed only forested areas, my team and I surveyed all types of landcover including forests and plantations.

Sampling design

I superimposed on the entire study area a 17x17 km grid and systematically selected 47 (~15% of the total possible) grid cells in which to conduct the detection, non-detection surveys. I used the landcover classification for the landscape available from WWF-Indonesia (Setiabudi 2006) to stratify the sampling by landcover type. The number of cells surveyed per landcover type was selected based on the proportion of their availability across the landscape. Selection of grid cells to represent each landcover type was conducted based on a stratified-random approach in which higher priority was given to grid cells that contain a larger proportion of the respective landcover type. However, in a few instances, due to logistical constraints, the team had to shift the survey areas.

My team and I conducted detection, non-detection sampling at two different scales. At the landscape-level, each site was represented by the 17x17 km grid cell, while sampling occasions were represented by ~40, 1-km transects. At a finer scale, I considered each 1-km transect as the site, and sampling occasions were represented by ten 100-m segments. This approach resembles the 'robust design' in capture-mark-recapture studies as described by Pollock et al. (1990). As such, it is possible to estimate not only the tiger's probability of occupancy at the 17x17 km grid level, but also probability of habitat use at a finer scale based on observations conducted at 1-km transect level (Hines et al. 2010).

To minimize observer bias and associated problems such as spatial autocorrelation in selecting the survey target area, my team and I applied two levels of randomization. First we randomly selected a 2x2 km sub-cell within each 17x17 km grid cell as part of the transect routes for each team. For a situation when more than one team covered the same 17x17 km grid cell, we selected an independent random 2x2 km sub-cell for each team to include in its survey. Second, we randomized the transect start-point by walking 200-m following a random azimuth from the end point of the previous transect or drop point from the last vehicle access. Field testing of this approach indicated that, in most situations, observers lacked the ability to predict what the conditions were like beyond 200-m from the previous end point. I believe this technique minimized observer bias in selecting areas to survey and minimized autocorrelations between consecutive transects. Further attempts to mitigate the impacts of spatial autocorrelation were done at the analysis stage detailed below.

Along transects the team surveyed areas deemed to have the highest likelihood of finding animal sign. The team intensively searched for tiger and prey signs on forest trails, sand beds, river banks, ridgelines, and other areas where tiger sign were likely to be found. We did this, instead of following a straight line as typically conducted in Distance Sampling (Buckland et al. 2001), because of the non-feasibility and ineffectiveness of tiger sign sampling following straight lines, proven through preliminary method-testing. When possible the team implemented the survey in such a way that transect routes covered a gradient of values for covariates such as human disturbance within the 17x17 km grid cell, as represented by the distance-to-road or most-to-least disturbed scores.

Animal sign and environmental/habitat conditions

In each 17x17 km grid cell, my team and I conducted sign surveys (mainly for tracks and scats)

in 40, 1-km transects except in two grids where we could conduct the survey in only 29 and 32 transects due to logistical constraints. Each transect was divided into ten, 100-m segments. To measure the distance walked we used hip chains with biodegradable string (in most surveys) or GPS tracking (in a few individually-owned plantations where canopy cover was relatively open allowing ample GPS satellite coverage). Sign surveys and measuring of environmental variables were conducted in every segment.

At the level of 17x17 km grid cell my team and I noted the landcover type of the survey target. Using Geographic Information System (GIS) software ArcGIS version 9.3.1 I extracted grid-level landscape variables described below. For every 1-km transect, the team noted the names and number of observers, the weather, and GPS coordinates for the start and end of each transect. Using GIS, I also extracted landscape variables associated with each transect as described below. At every 100-meter segment we measured the altitude using the barometric altimeter available in Garmin® GPS units, and we tallied the score for overall vegetation cover, canopy cover, sub-canopy cover, understory cover, and slope (Appendix 2.1a), plus we observed, assessed and scored the impact and/or risk of logging, encroachment, fire, settlement, and hunting.

Due to the uniqueness of plantation characteristics, we assessed additional variables for plantations collected at every 100-m segment that included estimates of age, tree diameter and height, intensity of plant husbandry, the presence or cover of plants other than the main commodity species, leaf-litter cover, level of human activity, intervals between individual plants, and planting rotation (Appendix 2.1b). I summarized the values from observations of every habitat variable conducted at 100-m segments and treated them as site covariates associated with each 1-km transect.

A guideline developed based on field-testing was used to assist observers in assigning habitat scores. When ambiguities in assigning scores were found between observers, my team and I averaged the values from all observers. I believe the variable scores we documented effectively depicted habitat conditions while being relatively practical to collect and can be used for rapid assessment with relatively low levels of training.

At each detection my team and I recorded species, sign type (e.g., direct sighting, track, scat/dung), distances from the start point of transect, and perpendicular distance from the center of the transect line. Detections of multiple signs from the same species in the same segment were noted as only a single detection. For this paper, I focus on tigers and reduced all such information into whether or not the animal was detected in a given segment (for analysis at finer-scale) or transect (for analysis at landscape-scale).

Environmental variables at the landscape level were extracted from GIS layers available from World Wildlife Fund (WWF) Indonesia GIS Unit. These include landcover data produced based on manual interpretation of satellite images (Landsat TM-5, Landsat ETM-7, and IRS-P6) which has a classification accuracy of 85% (Setiabudi 2006); roads (updated from original data from Indonesian national survey and mapping coordinating agency - BAKOSURTANAL); and boundaries of conservation areas, boundaries of forestry concessions, and boundaries of agricultural concessions. I also obtained several GIS layers available in the public domain such as Bioclim interpolated precipitation version 1.4 (Hijmans et al. 2005), freshwater (rivers, canals, and lakes data) from Digital Chart of the World downloaded through <http://www.diva-gis.org/gData>, and Digital Elevation Model/DEM from Shuttle Radar Topographic Mission/SRTM version 4 available from International Center for Tropical Agriculture/CIAT (Jarvis et al. 2004). A complete list of landscape variables derived from GIS, the original source,

and treatments to the data are presented in Appendix 2.1c.

Analysis

I used descriptive statistics to compare habitat use by tigers in different landcover types and across different values of environmental variables. I summarized tiger detections in different landcover types relative to survey effort. I compared values of variables between sites where tigers were detected and non-detected graphically by plotting the mean, range, and 95% confidence intervals. Furthermore, I also assessed tiger habitat selection without accounting for detection probability based on resource selection probability function (RSPF; Manly et al. 2002). The selection ratio is defined as: $\hat{w}_i = o_i/\pi_i$, where, \hat{w}_i represents the estimated selection ratio or resource selection function (i.e., the proportion of the population of available resource units in category i that are used); o_i represents the proportion of the sample of used resource units that are in category i ; and π_i represents the proportion of available resource unit that are in category i . For both graphical plots and RSPF calculations, I determined significant differences in the mean value based on non-overlapping 95% confidence intervals.

I used Program PRESENCE (Hines 2006) to estimate the probability of occupancy ($\Psi_{17 \times 17 \text{ km}}$) for tigers across landcover types at the landscape level. Using a similar approach, I also assessed habitat use by tigers within each landcover type where adequate tiger detection data were collected, based on the probability of use ($\Psi_{1\text{-km}}$) at the finer spatial scale. PRESENCE uses the models developed by MacKenzie et al. (2002; 2003) and others (such as Hines et al. 2010 for the spatial autocorrelation model) to estimate the probability-of-occupancy or probability-of-use from detection-non-detection data collected in a series of patches, sites and/or grid cells.

I modeled the effects of different covariates (i.e., landscape, habitat, and environmental variables) on tigers' probability of occupancy ($\Psi_{17 \times 17 \text{ km}}$) or habitat use ($\Psi_{1\text{-km}}$). Using a logistic

model and logit link in PRESENCE, I considered covariates as the independent variables and investigated their influence on the probability of occupancy/habitat use as the response variables.

The logistic model can be noted as follows (MacKenzie et al. 2006):

$$\text{logit}(\Psi_i) = \ln\left(\frac{\Psi_i}{1-\Psi_i}\right) = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_u x_{iu}$$

or,

$$\Psi_i = \frac{\exp(\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_u x_{iu})}{1 + \exp(\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_u x_{iu})}$$

where

Ψ_i = the probability of occupancy, or probability of use for i th sampling unit

x_i = value for covariate u measured at i th sampling unit

β = regression coefficient that determines the size of the effect of the respective covariates, which are to be estimated; β_0 is the intercept term.

i = number of sampling units or sites

u = number of covariates entered into the model.

Detection (1) and non-detection (0) data collected from all sampling occasions (1-km transects for landscape-level tiger occupancy, or 100-m segments for habitat use) in all sites (17x17 km grid, or 1-km transect, respectively) were organized into a vectors of detection histories. As an example, a collapsed version of a detection history for the grid cell S02W01, is $h_{S02W01} = 10100110--$. This detection history indicates that out of ten possible sampling occasions (I collapsed data so that each occasion was represented by 4 km transects), surveys were conducted only for the first eight occasions and tiger sign was detected in occasions 1, 3, 6, 7 but not in occasions 2, 4, 5, 8. In this case, there was no survey conducted for occasions 9 and 10 as indicated by a dash (-). These occasions or replicates are treated simply as missing values in the detection history data where detection probability is not modeled and hence will not affect the overall estimates of parameters (Hines 2006).

I analyzed the data at two levels. At the mega-landscape level, I treated each 17x17 km

cell as the ‘site’, while each 1-km transect represented a sampling occasion. As the 17x17 km grid size was considered close to the animal’s home-range size, the landscape-scale analyses were therefore expected to reveal the ‘true occupancy’ for tigers. To investigate the tiger’s habitat-use within certain landcover types, I considered each 1-km transect as the ‘site’ while the 100-meter segments represented ‘replicates.’

Prior to using the covariates to develop occupancy models, I explored the correlations between them as a means of understanding the nature of the variables and, when necessary, to reduce the number of covariates used for the next stages of analyses to avoid redundancy. I considered variables to be highly correlated when correlation coefficients were higher than 0.6 (Green 1979, Gaveau et al. 2009). For highly correlated variables, I selected the one considered most representative based on its ecological relevance, availability across wider area, ease of collection, or a combination of these.

Developing a spatially-explicit landscape-scale tiger occupancy model

To develop spatially-explicit models at the landscape scale I treated each 17x17 km grid cell as the site for which I would estimate the tigers’ probability of occupancy. Preliminary analysis revealed that collapsing the detection history data from 40 to 10 occasions reduced the number of zeros in the data and stabilized the numerical algorithms used in Program Presence. After collapsing, each occasion represents 4 consecutive 1km transects.

I used GIS software ArcGIS version 9.3.1, to extract site covariates such as distance to forest edge, deforestation rate within grid cells, distance to deforested area, forested area within grid cells, altitudes, slopes, distance to forest centroids, distance to centroids of protected areas, distance to major public roads, distance to all public roads, and precipitation (Appendix 2.1c). Due to the relatively low number of samples at the landscape-level (i.e., 47, 17x17 km sites), it

was not feasible to include all available covariates in the occupancy model (Green 1979, Guthery and Bingham 2007). Hence, considering the correlation between variables and using *a priori* knowledge related to tiger ecology, I ensured that the number of covariates used in the models was no more than 20% of the number of sites.

Following the above procedure, I retained 7 GIS-based landscape-scale continuous variables (hereafter ‘grid-level landscape variables’) used to model the probability of occupancy ($\Psi_{17 \times 17 \text{ km}}$). The variables were: 1) forest area within each grid cell based on the condition in 2007 (“For07Area”), 2) rate of deforestation from 2006 to 2007 for each 17x17 km grid cell (“Def0607”), 3) altitude based on Digital Elevation Model/DEM (“AltDEM”), 4) average distance to forest centroids (defined as the centroid of contiguous forest area equal to or greater than 50,000 ha based on conditions in 2005; “DtF05Cr”), 5) average distance to the centroid of protected area (“Dtpacr”), 6) average distance to major public road (“Dtmprd”), and 7) interpolated precipitation averaged for each grid cell (“Precip”). In addition, I also used the categorical variable of landcover type (“LCCode”) or forest/non forest category (“LCFor”) to model the detection probability of the animal. Records for the seven continuous variables are available for all the grid cells across the landscape; while the categorical landcover type or forest/non-forest variable is available for only the surveyed grids. Based on the correlation coefficients, these continuous variables have relatively weak correlations with each other (all combinations Pearson $r < 0.6$; Appendix 2.2a).

Program Presence uses the logit link transformation to force estimates of probability of occupancy (Ψ) to be between 0 and 1. This involves the use of an exponential function as shown above, which handles smaller values of covariates better than larger ones. When used in exponential terms, large covariate values can easily cause numerical calculation problems. As

such, values for each variable were normalized and/or scaled by computing z-values ($(x - \bar{x})/sd$) as a means of covariate transformation, while scaling was done by dividing the covariate value by a constant (Jim Hines/USGS, pers. comm.).

I developed occupancy models using Program PRESENCE and used the estimates of tiger occupancy ($\Psi_{17 \times 17 \text{ km}}$) from the best model to construct spatially-explicit models predicting occupancy across the landscape, including the un-surveyed areas. Using the selected covariates, I developed a set of models to assess the influence of each variable on $\Psi_{17 \times 17 \text{ km}}$. I modeled probability of occupancy as a function of the above listed seven variables as a univariate model. For each case, I modeled the detection probability (p) as either constant (.) or influenced by two-category landcover type (lcfor) coded as forest (1) or non-forest (0). My *a priori* predictions were that tiger occupancy would increase as the proportion of the forested area within the grid increases, as the rate of deforestation declines, as altitude declines, as distance to forest centroid and distance to protected area centroids decline, as distance to public roads increases, and as precipitation increases. In terms of the relative influence on tiger occupancy, I predicted the most influential to the least influential covariates would be: proportion of forest, distance to public roads, altitude, precipitation, distance to forest centroids, distance to protected area centroids, and rate of deforestation. I also predicted that landcover type would influence detection probability of tiger signs.

In building each model set, first I entered each variable in a univariate model. Based on the performance of the univariate models I constructed multivariate models using combinations of covariates and included at least one of those covariates that performed relatively well in univariate models, similar to the approach suggested by Thomas et al. (Thomas et al. 2010). Models were ranked and evaluated based on Akaike Information Criteria - AIC (Burnham and

Anderson 1998). To evaluate and mitigate the impact of spatial autocorrelation in the detection history data on the parameter estimates, I also ran custom models incorporating spatial autocorrelation (Hines et al. 2010). Meanwhile, spatial autocorrelation between 17x17 km grids on tiger detection rate, on values of covariates, and on the estimates of probability of occupancy were assessed based on Moran's I statistic performed in ArcGIS version 9.3.1 using its default options.

I selected the best model based on AIC and used the estimates of probability of occupancy for each grid cell to construct a spatially-explicit tiger distribution model across the landscape. I evaluated the uncertainty in the estimates based on the coefficient of variation (standard errors divided by the estimate of occupancy) for each cell. As a simple way to verify that the program had run properly, I contrasted the averages of the occupancy estimates from the best model between grid cells where tigers were detected and not detected. I considered that the program ran as expected if sites where tiger sign was detected were predicted to have higher mean of predicted probability of occupancy over sites where tiger sign were not detected. Unlike species distribution modeling based on presence-only data, model verification using independent data is not a simple procedure when detection is imperfect.

In the resulting map depicting the probability of tiger occupancy in each grid cell across the landscape, I highlighted un-surveyed cells that have covariate values far beyond the range of the surveyed cells. For example, although actual surveys were conducted in elevations ranging from 0 to 1,250 m (measured directly in the transect), the highest average elevation of the surveyed cell was below 500 m above sea level (based on DEM calculated in GIS); hence I had little confidence in the prediction of tiger occupancy for grid cells that had average elevations far beyond that range. In the resulting map, as a warning in the interpretation, I highlighted cells

where average elevation was higher than 750 m.

Assessing tiger use- and selection-of-habitats within forest and plantation areas

Estimates of the occupancy or probability of use at the patch or within-habitat scale are essentially equivalent to the resource selection function (RSF) or, depending on the sampling design, resource selection probability function (RSPF) (Boyce and McDonald 1999, MacKenzie et al. 2006). The RSF is proportional to, while RSPF directly represents, the probability of a resource unit being used (Boyce and McDonald 1999). Methods of estimating the RSPF are based on presence-absence data assuming that a non-detection is an absence. Therefore, occupancy techniques can produce more accurate estimates of the probability of habitat use by incorporating detectability.

At a finer spatial scale, sample units were represented by 1-km transects, augmenting the number of samples by an order of magnitude. A larger sample size allows us to investigate not only the tiger's use- or selection-of-habitat across landcover types but also within selected landcover types containing adequate records of tiger detections. I developed habitat use ($\Psi_{1\text{-km}}$) models using different sets of covariates including a) variables extracted in GIS from 500-m radii of the start- and end-point of each 1-km transect (values from both circles were averaged), hereafter 'landscape covariate' b) variables scored directly in the field and tallied in each transect in all landcover types, hereafter 'manual covariates' and c) specific variables observed and tallied only in plantation areas, hereafter 'manual plantation-specific covariates.' I also combined sets of covariates to model tiger habitat use ($\Psi_{1\text{-km}}$) either for 1) all landcover types, 2) forest only, or 3) specific plantation where adequate tiger detections were obtained (i.e. acacia).

Within each landcover-type, habitat use models were developed for natural forest and acacia plantations only. I could not develop models for other landcover types due to the small

number of tiger detections. For those, I focused on qualitative rather than quantitative analysis.

Using the occupancy modeling approach, I developed habitat use models by incorporating the effect of different covariates with similar procedures used to develop the landscape level occupancy models. I extracted the estimates of the probability-of-habitat-use ($\Psi_{1\text{-km}}$) from the best models to calculate the likelihood ratios of habitat use between landcover types. Meanwhile, I also used the untransformed estimates of coefficients for covariates (β) to evaluate the effect of different variables on the probability of habitat use ($\Psi_{1\text{-km}}$) by tigers. I considered a covariate to have a strong impact on Ψ if its respective estimate of β has 95% confidence limits (calculated as $\hat{\beta} \pm 1.96 \times \text{SE}$) that did not include zero (Dupont 2002).

To account for uncertainty in model selection, I used model averaging technique to calculate the weighted average of beta estimates and the unconditional standard errors (Buckland et al. 1997, Anderson 2008).

RESULTS

Summary of effort

My team and I systematically surveyed 1857 km of transects in 47 17x17 km grid cells covering six different landcover types (Table 2.1). Tiger sign was detected in all but two landcover types: mixed agriculture and coconut plantation.

Habitat selection, use and characteristics assuming perfect detection

In analyzing the tiger's habitat selection ratio (\hat{w}) for different landcover types, differences between forest and plantations only became statistically significant when considering finer spatial-scale observations for which I had a larger number of samples. Although differences in the means of habitat selection ratio (\hat{w}) between landcover types were apparent, none was statistically significant at the 17x17 km grid-level (Figure 2.2a & b) even when data from all

plantations were combined (Figure 2.2c). At the finer scale of 1-km transects, tigers significantly selected forest over plantations (Figure 2.2c), particularly over oilpalm, rubber, and others that were not documented to be used (Figures 2a & 2b).

Sites where tigers were detected at the 1-km transect scale in acacia were significantly closer to water compared to sites where tigers were not detected (Figure 2.3). In forests the results were opposite. In acacia plantations, compared to sites without tiger detections, sites with tiger detections were closer to forest centroids, closer to protected area centroids, and – contrary to *a priori* prediction – closer to major public roads. In forest areas, I found only slight differences between sites with tiger detections and non-detections in terms of precipitation, distance to forest centroid, and distance to freshwater.

Using manual covariates collected at 100-m segment and averaged at the 1-km transect scale, I found that in acacia plantations, sites with tiger detections had higher overall vegetation cover scores, slightly thicker understory cover, and significantly higher sub-canopy cover scores compared to sites where tigers were not detected (Figure 2.4). In forest areas, only understory cover was significantly thicker in sites with tiger detections compared to sites without. Both sites with and without tiger detections had similar canopy-, sub-canopy-, and overall vegetation cover. I found no apparent difference in human disturbance level between sites with and without tiger detections in forest and other landcover types, except in acacia. In these plantation areas, sites with tiger detections had significantly lower levels of logging activity and had higher levels of encroachment risk, but lower levels of fire risk compared to sites without tiger detections (Figure 2.4b). The terrain in plantation sites (acacia, oilpalm, and rubber) with tiger detections had significantly gentler slopes, while in forest areas the results were opposite (Figure 2.4c).

Comparison of plantation-specific covariates at the 1-km transect scale was possible for

only acacia and oilpalm, which had sufficient tiger detection data. Acacia plantation sites with tiger detections had significantly older plants, significantly taller trees, significantly lower levels of husbandry (plantation management), significantly higher plant biodiversity, significantly higher leaf litter, and significantly lower levels of human activity (Figure 2.5a). There were no differences between the sites in terms of distance between plants (plant interval) and number of rotations. In contrast, oilpalm plantation sites with tiger detections were significantly younger in plant age compared to sites without tiger detections. Similar to acacia plantations, sites with tiger detections in oilpalm plantations also had significantly higher score for other plant diversity (Figure 2.5b).

Occupancy models

Models for probability-of-tiger-occupancy ($\Psi_{17 \times 17 \text{ km}}$) were developed using seven grid-level covariates that had low correlation to each other (<0.6 ; Appendix 2.2a). The best model included 2 variables: altitude (AltDEM) and distance-to-forest-centroid (Table 2.2). Based on the beta estimates, tiger probability-of-occupancy ($\Psi_{17 \times 17 \text{ km}}$) increased significantly with altitude, and decreased but not significantly with distance-to-forest-centroids (Table 2.3). Relative estimates of betas for every grid-level landscape covariate were robust (consistent +/- direction) across different scenarios, including the univariate models and model average (Table 2.3).

Spatially explicit occupancy model

Using the best model from the model set above, I then developed spatially-explicit predictions of tiger occupancy across the landscape (Figure 2.6). This prediction shows that sites with higher probability of occupancy were concentrated in the western- and southern-parts of the study area. The model generally has low confidence (large standard error) in predicting tiger occupancy in peat swamp areas, which are located in the upper right (NW) of the study area.

The analysis showed that, using the same covariate(s), models accounting for spatial autocorrelations in detection histories within each site (Hines et al. 2010), always performed better than original models. Using Moran's I statistic (Table 2.4) to evaluate spatial autocorrelation between sites (at 17x17 km scale) in the landscape, I also found that values of covariates, counts of transects with tiger detections, and prediction of occupancy probability (17x17 km) were all significantly clustered (Z score > 3.28, $P=0.01$); however, tiger detection-non-detection was found to be random-to-clustered (Z score = 1.94, $P=0.1$).

Habitat use models

Across landcover types

To compare habitat use among landcover types I first assessed the relative importance of different landcover types in explaining the variation in tiger probability of detection (p) and occupancy (Ψ) (Table 2.5). I found that the best model included LCCode (the landcover coded that corresponds to the distance to and dissimilarity from the forest). This model performed better than those accounting for differences between landcover types as simply categorical (0 or 1). Therefore, I included LCCode as an additional covariate to model p or Ψ .

Lumping landcover types together, I modeled tiger habitat use ($\Psi_{1\text{-km}}$) using two different sets of covariates. First, based on landscape covariates, I found that models including only the LCCode were superior to other models (Table 2.6a). Beta estimates from the best model for LCCode indicate that probability of use ($\Psi_{1\text{-km}}$) by tigers significantly decreased as the landcover types increasingly became dissimilar or distant from forest (Table 2.7a). Beta estimates from univariate models under this analysis further indicated that probability of habitat use ($\Psi_{1\text{-km}}$) increased as altitude (AltDEM), distance-to-freshwater (Dtwater), distance to forest edge (Dtfedge07), and distance to major public roads (Dtmprd) increased, and that probability of

habitat use ($\Psi_{1\text{-km}}$) declined as precipitation (Precip) and distance to centroid of protected areas (Dtpacr) increased.

For the second model set based on manual covariates, I found that the best model included understory cover (understory), landcover code (LCCode), fire risk, settlement, slope, and altitude (Table 2.6b). The parameter estimates for the logit link function were positive and significant for understory and altitude, and negative and significant for landcover code and settlement (Table 2.7b). Estimates of these covariate parameters, especially in terms of the direction and value relative to the standard error, were also robust across models.

From the best model developed using landscape covariates, I compared the estimates of habitat use ($\Psi_{1\text{-km}}$) among six landcover types. The ratio of probability-of-use by tigers, relative to forest, decreased from acacia, oilpalm, rubber, mixed-agriculture, and coconut (Figure 2.8a). From the best model developed using manual covariates, I also compared the estimates of habitat use ($\Psi_{1\text{-km}}$) between six landcover types. I found that forest was most used followed by acacia, oilpalm, rubber, mixed agriculture, and coconut (Figure 2.8b). Though slightly different in the value, the rank of the landcover types in regard to probability of use by tigers remained consistent with results under the first set of covariates.

Within forest habitat selection

Based on the first set of models developed using landscape covariates, I found that distance-to-freshwater (Dtwater) was the single most important variable determining probability of habitat use by tigers within natural forest areas (Table 2.8a). The beta estimate for this covariate indicates that, within forest areas, tiger significantly selected sites that were farther from water contrary to my *a priori* prediction (Table 2.9a). Furthermore, based on univariate models developed with the rest of the landscape variables, I found that within the forest areas, tigers

tended to use areas with higher elevation, lower annual rainfall, farther from forest edge, and closer to forest centroids.

Based on models developed using manual covariates, I found four variables (understory cover, encroachment, settlement, and slope) to be the most important factors determining tiger probability of habitat use within forest areas (Table 2.8b). All of those variables had statistically significant effects on tiger probability of habitat use (Table 2.9b). Tigers significantly preferred forest with denser understory cover and steeper slope, and they significantly avoided forest areas with higher human influence in the forms of encroachment and settlement. After obtaining this result, I further explored the effect of slope on the tiger's detection probability (p). I found that accounting for slope in modeling detection probability “psi(understory+encroach+Settlement),thta0, thta1,p (Slope)” produced models that performed better than the best *a priori* model (delta AIC = 5.23), which accounted slope in the probability-of-occupancy instead of – detection (“psi(understory+encroach+Settlement+Slope), thta0,thta1,p(.)”). Beta estimates (β [SE]) from this new model for slope as a detection covariate was 12.25 (4.59) meaning that the probability of detecting tigers significantly increases with slope.

Within acacia plantation habitat selection

Using landscape covariates, I found distance-to-freshwater and distance-to-major-public-road as the most important variables determining tiger probability of habitat use within acacia plantations (Table 2.10a). In contrast to forest areas however, within acacia plantations tigers tended to use areas closer to water (Table 2.11a).

Using manual covariates, I found four variables (slope, sub-canopy cover, encroachment, and logging) to be the most important factors determining habitat use by tigers in acacia plantations (Table 2.10b). Of these four variables, it was only logging, however, that had a

significant impact (Table 2.11b). Tigers significantly avoided areas with higher logging activity, and avoided, though not significantly, steeper areas. In acacia plantations, tigers preferred, although not significantly, areas with thicker sub-canopy cover and with higher level/risk of encroachment.

Based on covariates collected in the plantation areas only, three variables (plant age, human activity, and leaf litter) were found to be the most important in determining tiger habitat use in acacia plantations (Table 2.10c). Tigers preferred areas with older plants and more leaf litter; and avoided areas with high human activity. Beta estimates from univariate models show that tigers significantly preferred areas with taller trees, and significantly avoided areas with higher intensity of plantation management activity (Table 2.11c).

I descriptively summarized the few records of tiger detections from oilpalm and rubber plantations as they provide some rare evidence on the use of such areas by tigers. In oilpalm plantations, tiger sign was detected only in two locations that were measured respectively ~13 and ~7.5 km from the edge of the nearest large (>50,000 ha) forest block. The only record of tiger sign in the rubber plantations was documented in a site that was ~16 km away from the edge of the nearest large forest blocks (Figure 2.9).

DISCUSSION

Tiger occupancy and habitat use in Central Sumatra

Based on their impacts on tiger occupancy and habitat use, I classified covariates into three different categories. The first category includes covariates that had consistent, positive or negative impacts across different scales. The second category includes covariates whose impacts depend on the scale and context. The last category contains covariates that had no apparent impacts based on the models I developed in this study.

Scale independent factors

Understory cover was consistently found to have positive impacts on tiger probability of occupancy and habitat use across the landscape and within different types of landcover. This suggests that availability of adequate vegetation cover at the ground level served as an environmental condition fundamentally needed by tigers regardless of the location. As an ambush hunter (Sunquist et al. 1999) tigers need cover. Without adequate understory cover, tigers would find it hard to capture their prey, even if prey animals are abundant. It can be expected, therefore, that lack of understory cover would eventually impact tiger reproductive and survival rates. Furthermore, without adequate understory cover, tigers are even more vulnerable to humans who generally perceive them as a potential danger and therefore readily persecute them. Although this likely applies to all tigers, it is particularly relevant to Sumatran tigers. Perhaps human persecution of adventurous tigers (Boomgaard 2001, Nyhus and Tilson 2004) has become an important selection factor contributing to the overall secretive behavior of tigers in the region, causing this obligatory requirement for ample understory cover.

Variables that represent distance or dissimilarity from forest such as landcover rank (LCCode) and distance-to-forest-centroid (Dtf05cr), also consistently impacted tiger probability of occupancy or habitat use. As the site or landcover type became more dissimilar from forest or was further from the centroid of large forest blocks, occupancy or habitat use decreased. The impact of landcover rank, which was used only to model tiger probability of habitat use ($\Psi_{1\text{-km}}$) across different land cover types, was always significant. Beta estimates for distance-to-forest-centroid also were consistently negative. These results indicate that although tigers were capable of using some plantation areas, forest remained their core habitat without which they are unlikely to survive in Sumatra.

I found that human-disturbance-related variables negatively affected tiger occupancy and habitat use. In the northern part of Sumatra (Griffith and van Schaik 1993), tigers and several other animal species were found to be very sensitive to human activities. In occupancy models human disturbance was represented by GIS-extracted landscape variables ‘distance to deforested area’, ‘distance to forest edge’, and ‘distance to major public roads’ while at the micro-habitat scale by variables ‘settlement’, ‘encroachment’, ‘logging’, and ‘hunting.’ Of the specific covariates collected only in plantation areas, ‘husbandry’ and ‘human activities’ negatively affected tiger occupancy. However, not all effects of these variables were statistically significant. Those variables with statistically significant impacts on tiger occupancy or habitat use include a) ‘settlement’ in the best and univariate habitat use models, both within forest areas and across six landcover types; b) ‘encroachment’ in the best and univariate models for tiger habitat use within forest areas; c) ‘logging’ in best and univariate models for habitat use within acacia plantations; and d) ‘husbandry’ in univariate model for habitat use within acacia plantations.

Depending on the context, however, human disturbance could take different forms in different landcover types. In forest areas, sites with a large encroachment score generally had higher levels of human activity. This was not always the case in plantation areas. In acacia plantations, areas with higher encroachment scores were typically those that had lower levels of plantation care management activities and could actually have lower levels of human activity. This typically happened in areas considered by plantation managers to be less productive such as those with unresolved land status. Highly encroached areas in acacia plantations, therefore, did not necessarily have higher levels of human activity.

Scale dependent factors

The impact of altitude on tiger occupancy or habitat use depended on the scale of analysis and the context. I found that probability of tiger occupancy increased with altitude. At the landscape-level over all landcover types, the effects of altitude on tiger habitat use were nearly significant for grid-based landscape variables and significant for manual habitat variables. Within forest areas, the impacts were still positive, but became less significant for both landscape variables and manual variables. In acacia plantation, the model failed to converge when I used altitude as a landscape variable, and had a small estimated impact ($\hat{\beta}=0.16[SE=0.35]$) when I used altitude data from manual variables.

I suspect that altitude, which in the study area strongly correlated with slope, was negatively confounded with overall human activity. In Sumatra humans generally utilize lower altitude with more gentle terrain before they move up to higher altitude. It is not surprising, therefore, that most of the remaining forests, particularly those growing on mineral soils, are at higher altitudes. Because of the high demand for flat land at low elevation, forests in such areas in Sumatra were degraded at a much faster rate and therefore predicted to go extinct sooner than forest at higher altitudes (Holmes 2002).

The importance of altitude/slope on tiger occupancy may also be driven by the fact that peat swamps dominated the low-lying forest types in the landscape. Such forest types are generally lower in quality in comparison to mineral soils forests due to the low level of primary productivity (Whitten et al. 2000) of peat swamps which do not support ungulate community biomass. In addition, large ground-living animals, particularly those with pointed feet such as most ungulates, face further challenges travelling in peat land terrain due to the soft ground and porous texture. Field research conducted in such areas suffers from low detectability of animals due to lack of obvious animal trails and spongy, porous substrate that is poor for tracks. Previous

work documented an extremely low abundance of potential prey in peat land areas and found mainly those prey animals that were capable of utilizing higher forest strata for movement or foraging.

The additional post-hoc models that included slope for tiger detection probability, instead of occupancy, were superior based on AIC rankings. This suggested that within forest areas tigers are more easily detected in steep-terrain. Therefore it is important to determine if tigers preferred such areas, or rather that detection was easier due to constricting or funneling animals along the strip of a narrow ridge or valley. Reducing observer detection bias could be done by fully randomizing the area surveyed including randomizing transect direction and not allowing observers to select areas with higher probability of finding animal sign. While such an approach might be statistically more sensible, given the very low detection probability and logistical constraints, is not likely to be practical and modeling approaches that compensate for this bias are a better approach.

Distance-to-freshwater had significant yet inconsistent impacts on tiger probability-of-use in different landcover types. I suspect that this variable might be again confounded with human activity (for forest areas and overall landcover) or understory vegetation cover (for acacia plantation areas). Tigers avoided areas closer to water across all landcover types, and more significantly in forest areas, but they significantly preferred sites that were closer to water in acacia. Water availability is not actually a critical issue for tigers in the landscape. This region already has relatively high annual rainfall (more than 2210 mm/year from 2004 to 2006). Additionally most sites within the study area also had a dense network of streams in the upper lands, or wider rivers and other water bodies such as lakes or swamps in the low lands.

Less-influential factors

Variables that were never identified as important at any scale include three covariates representing vegetation cover namely “canopy”, “sub-canopy”, and “overall” that were measured in the field in all landcover types, and “rotation” and “plant interval” that were quantified during surveys only in plantation areas. Except for understory, no vegetation-related characteristics were important determinants of tiger use. This result suggests that, with other factors (particularly human disturbance) being equal, tigers not only used but seemed to prefer forests that were selectively logged or slightly disturbed, as they tended to have thicker understory cover compared to mature primary forest. For the tiger, restoration of previously disturbed or logged forests should not focus on achieving ‘climax’ primary forest condition. Instead, reducing the level of human disturbance and maintaining adequate understory cover would likely be more beneficial for tigers.

The fact that “rotation” and “plant interval” did not impact tiger use in this study was mainly due to low variation in these variables. Most oilpalm and acacia plantations in the study area were only in their first rotation with few in the second. For the varieties of acacia (*Acacia mangium*, *A. crassicarpa*, or *A. auriculiformis*) planted in the landscape, each rotation typically takes about 7 years, with intensive management taking place in the first 2 to 3 years. The period after intensive management had ceased and just before the timber was harvested appeared to be the time when tiger use was maximized. That was likely related to the low levels of human activity during this time and the relatively higher plant diversity at the ground level that served as better cover for tigers. The oilpalm varieties planted in the study area were *Elaeis guineensis dura*, *E.g. picifera*, and *E.g. tenera*. These plants typically start to bear fruit about 3 years after planting and remain productive for about 20 years. Before bearing fruit, oilpalm plantations typically had relatively low levels of human activity. Meanwhile, oilpalm plant intervals (mean=

4.3 m, SD=0.25) were significantly ($t=214.5$, $P<0.001$) greater than acacia plant intervals (mean=2.9 m, SD=0.21). This permits sunlight penetration to ground level allowing pioneer vegetation to flourish. Meanwhile, human activities are relatively low in young oilpalm plantations before fruiting. These are reasonable explanations for why tigers are more likely to use younger rather than older oilpalm plantations.

Landscape-scale assessment: occupancy models and spatially-explicit predictions

At the landscape-scale, I found that altitude and distance-to-forest-centroid were the important determinants for tiger occupancy. Closely-competing models suggest that proportion of forest within grid cell (“For07area”) was also an important factor, while distance-to-centroid-of-protected-area was the next most important factor. Distance-to-road, which was identified as the most important factor representing human disturbance in a previous study in the neighboring landscape of Kerinci-Seblat (Linkie, Chapron et al. (2006), but was not an important factor in this study. Unlike that previous study, my models included other variables that represented not only human disturbance (such as roads and deforestation) but also terrain- and climate-related properties (altitude), water availability (precipitation, distance to freshwater), and general habitat quality (proportion of forest in a grid cell and distance-to-forest-centroids). Additionally, my study assessed tiger occupancy and habitat use across different landcover types and not just in forest areas. Furthermore, other landscape characteristics such as variation in forest types, extent and relative position of landscape features (especially public roads relative to forest blocks) appear to be very different between the Kerinci-Seblat and my study area.

Based on the spatially-explicit model, many areas with high probability of tiger occupancy were located outside of the existing protected areas. Areas with high estimated probability of occupancy and with high precision (low standard error) of the prediction were

concentrated in the southwestern part of the landscape. The model also predicted higher elevation areas to have a higher probability of tiger occupancy. Even after excluding those areas with values well beyond the range of surveyed altitude values, the map still predicted relatively large areas with very high probability of tiger occupancy, particularly to the northwest of Rimbang Baling Reserve. In contrast, although with lower precision, current protected areas in peat land (i.e., Kerumutan Wildlife Reserve/KWR) had little area with a high probability of tiger occupancy. Interestingly, areas with the highest probability of occupancy in peat land were located to the east of KWR, on the Kampar Peninsula, and on the western part of Bukit Tigapuluh, are currently not protected. In fact, large portions of these areas were proposed for, or already in the process of, conversions by either pulp-and-paper- or palm-oil-producing companies (e.g., Uryu et al. 2010, Warsi et al. 2010).

More intensive surveys are required to obtain better precision in occupancy estimates, particularly for the peat land areas. Low occupancy with large standard errors could be due to combination of ecological factors and survey difficulties. Surveys in such an area were challenged by both mobility/accessibility and the low probability of detecting animal sign. Further surveys and alternative methods that can overcome the challenges of ecological investigation in such a poorly studied habitat should be explored. For example, it might be possible to improve sign detection by using [baited] track stations (Ray and Zielinski 2008), or using trained dogs (MacKay et al. 2008) to assist in sign detection of target species.

The spatially-explicit model developed in this study could serve as the basic framework for developing a tiger conservation vision at the mega-landscape-scale. To maximize the likelihood of success in tiger conservation, priorities should be directed toward securing those areas with highest probability of occupancy through protection and improved management.

Critical areas, for example those crucial for connectivity between two closely-located habitat blocks, could also be identified and managed to allow tiger dispersal. Further details of the mechanisms by which habitat protection and improvement can be achieved are discussed in Chapter 5.

Between and within landcover type: habitat characteristics, use and selection

In estimating tiger probability of use, different models consistently ranked plantations in the following order from best to worst: acacia, oilpalm, rubber, mixed-agriculture, and coconut. Such a ranking system is useful for tiger conservation, but should be considered within the context of the landscape studied rather than generalized to other study areas. These ranks are context specific representing a manifestation of complex and multidimensional characteristics associated with each landcover type. For example, while vegetation characteristics did play a role in determining occupancy and habitat use by tigers, so did other complex characteristics such as plantation age, historical impacts, managerial aspects of plantations, and extent and configuration of a particular type of plantation in the landscape in relation to proximity to forest blocks.

With context and scale recognized, rank can be used to prioritize the types of plantations in the landscape that should be managed to improve tiger conservation. The quality of habitat in each plantation could be improved. Timber/pulp-and-paper plantations such as acacia could be improved by regulating/reducing the level of human activities and increasing the coverage of understory vegetation. Each type of plantation should be able to facilitate the movement of tigers between patches of forest and prey were available in most areas (except in peat land forests), including plantations where signs of wild boar were commonly found.

Certain individual animals - possibly sub-adult transients - did venture through plantation areas relatively far from core forest habitat areas. Likely factors that motivated dispersal include the 'push' from the territorial-holding adults and 'pull' from the availability of habitable spaces, prey, and possibly mates in other places (Sunquist 1981, Diamond 2005). Such movements likely were facilitated by the existence of riparian areas that served as corridors, the availability of small patches of forests that served as sort of 'stepping stones', and the mosaic of plantations with adequate understory cover that provide habitat connectivity. The rate of such dispersal could be enhanced by improvement of habitats within and beyond forests including the plantation areas.

Implications for management

This study shows the importance of scale and context in the assessment of tiger habitat use. For example, the same factor such as altitude can have different impacts depending on the scale of analysis. Additionally context can influence tiger occupancy as illustrated by the different impacts of distance to freshwater, which depended on the landcover type under consideration. The management of tiger habitats and populations, therefore, should correspondingly consider appropriate scale and context for a particular strategy or action. Once a broad-scale vision, for example tiger conservation at the mega-landscape, has been clearly defined, management goals can then be identified for specific areas at finer-scales. Considering the dynamic nature of the landscape, it is important to continuously evaluate the landscape conditions, including land conversion and plantation age and iteratively adjust conservation strategies and goals.

The comparisons of relative values of different landcover types can be used to improve the management of plantations with regard to tiger conservation and management. Existing plantations, particularly those that are forestry-based such as acacia, possessed high potential to

be reclaimed for additional tiger habitat. They also potentially can become corridors, stepping stones, or mosaics of connectivity to facilitate animal movement (Anderson and Jenkins 2006). Although the overall value for tiger habitat of any plantation was much lower than forests, management practices of acacia plantations can be adjusted so that tigers can still use the plantation areas without necessarily causing negative economic impacts. In addition, plantation concessions that border protected areas can potentially serve as a buffer to reduce human disturbance and provide additional forest protection.

The results show that, while prey appear to be available across plantation areas, the most basic requirements lacking from many areas and believed to limit tiger use of plantations, were adequate understory cover and low levels of human activity. If these two factors can be improved, especially radiating out from the main forest habitat, tigers likely will start occupying these areas. Concurrently human-tiger conflict should be minimized through awareness, training, and education programs designed to build understanding and appreciation for wildlife among local people. If such an initiative is replicated across the landscape, tiger recovery is possible.

I found that tigers require habitats with some non-negotiable intrinsic characteristics such as understory cover and low levels of human activity such that, for these characteristics, ‘tigers cannot change their stripes.’ However, tigers can survive and possibly thrive even in human-dominated landscapes if such landscapes are managed for features that promote tiger existence and reduce human-tiger conflict. These conditions are necessary to accommodate this species in the landscape and thus prevent extinction of the Sumatran tiger.

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Table 2.1. Summary of survey effort and detection of tigers in five landcover types in Riau Province, Central Sumatra.

	Forest	Acacia	Oilpalm	Rubber	Mixed Agriculture	Coconut	Combined
<u>17x17 km GRID LEVEL</u>							
Number of 17x17 km grid cells surveyed	26	7	6	5	2	1	47
Grid cells with tigers detections	19	3	2	1	0	0	25
Probability of Site Occupancy ($\Psi_{17 \times 17 \text{ km}}$): Naïve estimate	0.73	0.43	0.33	0.20	0.00	0.00	0.53
<u>1-KM TRANSECT LEVEL</u>							
Number of 1 km transects surveyed	1029	268	240	200	80	40	1857
Transects with tiger detections	81	10	2	1	0	0	94
Probability of Site Use ($\Psi_{1\text{-km}}$): Naïve estimate	0.08	0.04	0.01	0.01	0.00	0.00	0.05

Table 2.2. Top models depicting tiger probability-of-occupancy ($\Psi_{17 \times 17 \text{ km}}$) at the landscape-scale with 17x17 km grid-level landscape covariates in Riau Province, Central Sumatra.

Model	AIC	Δ AIC	w_i	Model Likelihood	K
psi(AltDEM+dtf05cr),thta0,thta1; p(LCFor)	318.2	0.0	0.30	1.00	7
psi(AltDEM+dtf05cr+For07Area), thta0, thta1; p(LCFor)	318.9	0.7	0.21	0.69	8
psi(AltDEM),thta0,thta1; p(LCFor)	319.4	1.2	0.16	0.54	6
psi(AltDEM+dtf05cr+For07Area+ dtpacr) ,thta0,thta1,p(LCFor)	320.7	2.5	0.09	0.28	9
psi(dtf05cr),thta0,thta1,p(LCFor)	321.8	3.6	0.05	0.16	6
psi,thta0,thta1,p(LCFor)	321.9	3.7	0.05	0.15	5
psi(For07Area),thta0,thta1,p(LCFor)	322.0	3.8	0.04	0.14	6
psi(dtpacr),thta0,thta1,p(LCFor)	322.6	4.4	0.03	0.11	6
psi(Def0607),thta0,thta1,p(LCFor)	323.4	5.2	0.02	0.07	6
psi(Precip),thta0,thta1,p(LCFor)	323.8	5.6	0.02	0.06	6
psi(Dtmprd),thta0,thta1,p(LCFor)	323.9	5.7	0.02	0.06	6
psi(.),p(LCFor)	325.6	7.4	0.01	0.02	3
psi,thta0,thta1,p(.)	338.4	20.2	0.00	0.00	4

Psi=probability of site occupancy/habitat use; p=probability of detection; thta0= spatial dependence parameter representing the probability that the species is present locally, given the species was not present in the previous site; thta1= spatial dependence parameter representing the probability that a species is present locally, given it was present at the previous site. AltDEM= Altitude; dtf05cr= Distance to forest centroid; LCFor=Code for forest (1) or non forest (0); For07Area=Area of forest in the grid based on 2007 data; dtpacr=distance to centroid of protected area; Def0607=Deforested area from 2006 to 2007 in each grid cell; Precip=Precipitation; Dtmprd=Distance to major public road;

Table 2.3. Beta estimates for the logit link function for landscape covariates extracted using GIS based on best model, univariate models, and model average for tiger probability-of-occupancy ($\Psi_{17 \times 17 \text{ km}}$).

MODEL	Intercept	AltDEM	Dtf05cr	For07Area	Dtpacr	Def0607	Precip	Dtmprd
<i>A priori</i> relationship		-	-	+	-	-	+	+
Best (SE)	-7.63 (3.938)	<i>101.09</i> <i>(48.941)*</i>	-0.31 (0.220)	NA	NA	NA	NA	NA
Univariate (SE)	NA	76.72 (41.249)	-0.23 (0.185)	0.18 (0.119)	-0.27 (0.223)	-0.37 (0.490)	0.09 (0.358)	-0.11 (0.505)
Average (SE)	-5.311 (12.426)	72.361 <i>(1705.057)</i>	-0.178 (0.031)*	0.042 (0.006)*	-0.017 (0.010)	-0.008 (0.010)	0.002 (0.005)	-0.002 (0.009)

Note: * indicate statistical significance as defined by $\hat{\beta} \pm 1.96 \times \text{SE}$; italics indicate opposite from *a priori* prediction
 AltDEM=Altitude; dtf05cr=Distance to forest centroids; For07Area=Area of forest in the grid cell based on 2007 data;
 Dtpacr=distance to centroid of protected area; Def0607=Deforested area from 2006 to 2007 in each grid cell; Precip=Precipitation;
 Dtmprd=Distance to major public road.

Table 2.4. Moran's I index to evaluate spatial autocorrelations of covariates and estimates of occupancy ($\Psi_{17 \times 17 \text{ km}}$) for tigers at the landscape level based on data extracted from all surveys in 17x17 km grid cells in Central Sumatra.

Variable	Moran's I Index	Z Score	P	Notes
Counts of tiger detections	0.29	3.28	0.01	clustered
Tiger detection non detection	0.17	1.94	0.10	random to clustered
Occupancy ($\Psi_{17 \times 17 \text{ km}}$)	0.84	17.57	0.01	clustered
Standard Errors of $\Psi_{17 \times 17 \text{ km}}$	0.74	15.60	0.01	clustered
Distance to forest centroid	0.77	16.20	0.01	clustered
Forest area	0.60	12.64	0.01	clustered
Altitude	0.43	4.73	0.01	clustered
Distance to centroid of protected areas	0.33	3.64	0.01	clustered
Distance to major public road	0.40	4.56	0.01	clustered
Precipitation	0.74	7.74	0.01	clustered

Table 2.5. Comparison of tiger occupancy models for Central Sumatra that use different approaches for landcover coding in determining probability of detection (p) or occupancy (1-km): equal code (1) for different landcover (LC1 to LC6) vs. incremental scoring (1 to 6) of landcover according to its dissimilarity to forest (LCCode)

Model	AIC	Δ AIC	w_i	Model Likelihood	K
psi(LCCode),p(LCCode)	1499.75	0	0.8701	1	4
psi(LCCode),p(.)	1503.80	4.05	0.1148	0.132	3
psi(.),p(LC1+LC2+LC3+LC4+LC5+LC6)	1508.08	8.33	0.0135	0.0155	8
psi(LC1+LC2+LC3+LC4+LC5+LC6),p(.)	1512.88	13.13	0.0012	0.0014	8
psi(LC1),p(.)	1515.56	15.81	0.0003	0.0004	3
psi(.),p(LCCode)	1534.91	35.16	0	0	3
psi(.),p(LC2)	1541.41	41.66	0	0	3
psi(.),p(LC4)	1542.24	42.49	0	0	3
psi(LC4),p(.)	1543.51	43.76	0	0	3
psi(LC3),p(.)	1543.76	44.01	0	0	3
psi(.),p(LC3)	1545.95	46.20	0	0	3
psi(LC5),p(.)	1550.07	50.32	0	0	3
psi(.),p(LC5)	1550.07	50.32	0	0	3
psi(LC6),p(.)	1554.37	54.62	0	0	3
psi(.),p(LC6)	1554.37	54.62	0	0	3
psi(.),p(LC1)	1558.44	58.69	0	0	3
psi(LC2),p(.)	1730.19	230.44	0	0	3

Psi=probability of site occupancy/habitat use; p=probability of detection;
 LC1=forest, LC2=acacia, LC3=oilpalm, LC4=rubber, LC5=mixed agriculture, LC6=coconut
 LCCode: 1=forest, 2=acacia, 3=oilpalm, 4=rubber, 5=mixed agriculture, 6=coconut

Table 2.6. Top models ($w_i > 0$) for tiger probability of habitat use ($\Psi_{1\text{-km}}$) in Central Sumatra across all landcover types in the landscape based on detection history data collected at transect sites ($n = 1857$, 1-km transects) in six landcover types.

a) Developed using landscape covariates						
Model	AIC	Δ AIC	w_i	Model Likelihood	K	
psi(LCCode),thta0,thta1,p(LCCode)	1476.97	0	0.69	1	6	
psi(LCCode+altDEM+Precip),thta0,thta1,p(LCCode)	1480.02	3.05	0.15	0.21	8	
psi(LCCode+altDEM+Precip+dtwater),thta0,thta1,p(LCCode)	1480.41	3.44	0.12	0.18	9	
psi(LCCode+altDEM),thta0,thta1,p(LCCode)	1482.93	5.96	0.03	0.05	7	
psi(altDEM),thta0,thta1,p(LCCode)	1499.1	22.13	0	0	6	

b) Developed using manual covariates						
Model	AIC	Δ AIC	w_i	Model Likelihood	K	
psi(understory+LCCode+firerisk+Settlement+Slope+Altitude),thta0,thta1,p(LCCode)	1443.03	0	0.52	1	11	
psi(understory+LCCode+firerisk+Settlement+Slope+Altitude+encroach),thta0,thta1,p(LCCode)	1444.96	1.930	0.20	0.38	12	
psi(understory+LCCode+firerisk+Settlement),thta0,thta1,p(LCCode)	1446.16	3.130	0.11	0.21	9	
psi(understory+LCCode+firerisk+Settlement+Slope+Altitude+encroach+logging),thta0,thta1,p(LCCode)	1446.62	3.590	0.09	0.17	13	
psi(understory+LCCode+firerisk+Settlement+Slope),thta0,thta1,p(LCCode)	1447.00	3.970	0.07	0.14	10	
psi(understory+LCCode+firerisk),thta0,thta1,p(LCCode)	1450.78	7.750	0.01	0.02	8	
psi(understory+LCCode),thta0,thta1,p(LCCode)	1458.29	15.26	0.00	0.00	7	

Note: Psi=probability of site occupancy/habitat use; p=probability of detection; thta0= spatial dependence parameter representing the probability that the species is present locally, given the species was not present in the previous site; thta1= spatial dependence parameter representing the probability that a species is present locally, given it was present at the previous site. LCCode= landcover code; AltDEM= Altitude; Precip=Precipitation; dtwater=distance to freshwater; Dtfedge07=distance to forest edge; dtf05cr= Distance to centroid of forest block ; dtpacr=distance to centroid of protected area; Dtmprd=Distance to major public road; LCFor=forest(1) or nonforest(0)

Table 2.7. Beta estimates for the logit link function for different covariates based on best model and model average for tiger probability of habitat use (Ψ_{1-km}) in all landcover types in Central Sumatra.

a) Based on landscape covariates

MODEL	Intercept	LCCCode	AltDEM	Precip	Dtwater	Dtfedge07	Dtpacr	Dtmprd
<i>A priori</i> relationship	NA	-	-	+	-	-	-	-
Best (SE)	-3.06 (0.226)	-1.76 (0.304)*	NA	NA	NA	NA	NA	NA
Univariate (SE)	NA	-1.76 (0.304)*	<i>0.17</i> (0.091)	<i>-0.19</i> (0.105)	<i>0.18</i> (0.116)	<i>0.14</i> (0.104)	-0.13 (0.135)	<i>0.01</i> (0.111)
Average (SE)	-2.38 (0.109)	-1.77 (0.105)*	<i>0.61</i> (0.161)*	<i>-0.15</i> (0.029)*	<i>0.03</i> (0.009)	NA	NA	NA

b) Based on manual covariates

MODEL	Intercept	Under-story	LC-Code	Fire-risk	Settle-ment	Slope	Alti-tude	Encro-ach	Log-ging	Hun-ting	Sub-canopy	Canopy	Over-all
<i>A priori</i> relationship		+	-	-	-	-	-	-	-	-	+	+	+
Best (SE)	-15.50 (3.07)	0.67 (0.14)*	-1.28 (0.29)*	-0.52 (0.32)	-51.89 (12.81)*	-0.04 (0.15)	<i>0.32</i> (0.13)*	NA	NA	NA	NA	NA	NA
Univariate (SE)	NA	0.62 (0.12)*	-1.76 (0.30)*	-0.73 (0.31)*	-55.20 (2.12)*	<i>0.33</i> (0.11)*	<i>4.46</i> (0.79)*	-0.29 (0.17)	-0.20 (0.13)	-0.18 (0.16)	0.08 (0.13)	0.07 (0.13)	-0.06 (0.11)
Averaged (SE)	-15.25 (9.73)	0.65 (0.02)*	-1.32 (0.08)*	-0.52 (0.10)*	-50.81 (169.30)	-0.02 (0.02)	<i>0.25</i> (0.02)*	-0.01 (0.02)	-0.01 (0.00)	NA	NA	NA	NA

Note: * indicate statistical significance as defined by $\hat{\beta} \pm 1.96 \times SE$; italics indicate opposite from *a priori* prediction
 LCCCode=landcover code; AltDEM= Altitude; Precip=Precipitation; dtwater=distance to freshwater; Dtfedge07=distance to forest edge; dtpacr=distance to centroid of protected area; Dtmprd=Distance to major public road; Overall=overall vegetation cover

Table 2.8. Top models ($w_i > 0$) for probability of habitat use ($\Psi_{1\text{-km}}$) by tigers based on detection history data collected at transect sites within forest areas only ($n = 1029$) in Central Sumatra.

a) Developed using landscape covariates

Model	AIC	Δ AIC	w_i	Model Likelihood	K.
psi(dtwater),thta0,thta1,p(.)	1205.18	0	0.3906	1	5
psi(dtwater+Precip),thta0,thta1,p(.)	1205.82	0.64	0.2836	0.7261	6
psi(Precip),thta0,thta1,p(.)	1208.98	3.8	0.0584	0.1496	5
psi,thta0,thta1,p(.)	1209.01	3.83	0.0576	0.1473	4
psi(dtf05cr),thta0,thta1,p(.)	1209.35	4.17	0.0486	0.1243	5
psi(Dtfedge07),thta0,thta1,p(.)	1209.71	4.53	0.0406	0.1038	5
psi(altDEM),thta0,thta1,p(.)	1209.82	4.64	0.0384	0.0983	5
psi(dtwater+dtf05cr),thta0,thta1,p(.)	1210.31	5.13	0.03	0.0769	5
psi(Dtmprd),thta0,thta1,p(.)	1210.87	5.69	0.0227	0.0581	5
psi(dtpacr),thta0,thta1,p(.)	1210.98	5.8	0.0215	0.055	5
1 group, Constant P	1212.94	7.76	0.0081	0.0207	2

b) Developed using manual covariates

Model	AIC	Δ AIC	w_i	Model Likelihood	K
psi(understory+encroach+Settlement+Slope), thta0,thta1,p(.)	1172.06	0	0.3841	1	8
psi(understory+encroach+Settlement+Slope+ firerisk+Altitude),thta0,thta1,p(.)	1172.62	0.56	0.2903	0.7558	10
psi(understory+encroach+Settlement+Slope+	1174.05	1.99	0.14	0.3697	9

firerisk),thta0,thta1,p(.)					
psi(understory+encroach+Settlement+Slope+ firerisk+Altitude+Hunting),thta0,thta1,p(.)	1174.58	2.52	0.11	0.28	11
psi(understory+encroach+Settlement),thta0, thta1,p(.)	1176.25	4.19	0.05	0.12	7
psi(understory+encroach),thta0,thta1,p(.)	1177.34	5.28	0.03	0.07	6
psi(understory),thta0,thta1,p(.)	1190.35	18.29	0.00	0.00	5

Notes: Psi=probability of site occupancy/habitat use; p=probability of detection; thta0= spatial dependence parameter representing the probability that the species is present locally, given the species was not present in the previous site; thta1= spatial dependence parameter representing the probability that a species is present locally, given it was present at the previous site. Dtwater=distance to freshwater; Precip=precipitation; dtf05cr=distance to centroid of forest block; dtfedge07=distance to forest edge; altDEM=altitude; Dtmprd=distance to major public road; dtpacr=distance to centroid of protected areas

Table 2.9. Beta estimates for the logit link function for different covariates based on best model, univariate models and model average for tiger probability of habitat use ($\Psi_{1\text{-km}}$) within forest areas in Central Sumatra.

a) Based on landscape covariates											
MODEL	Intercept	AltDEM	Precip	Dtwater	Dtfedge07	Dtpacr	Dtmprd	dtf05cr			
<i>A priori</i> relationship	NA	-	+	-	+	-	-	-			
Best (SE)	-1.807617 (0.195492)	NA	NA	<i>0.289483</i> <i>(0.119699)*</i>	NA	NA	NA	NA			
Univariate (SE)	NA	<i>0.130293</i> <i>(0.117237)</i>	<i>-0.177834</i> <i>(0.124479)</i>	<i>0.289483</i> <i>(0.119699)*</i>	0.135160 (0.116786)	<i>0.021054</i> <i>(0.124197)</i>	-0.048251 (0.130231)	-0.167380 (0.131841)			
Average (SE)	-1.791841 (0.037916)	<i>0.0050033</i> <i>(0.001035)*</i>	-0.0524 <i>(0.009030)*</i>	<i>0.1999997</i> <i>(0.013156)*</i>	0.005487 <i>(0.001085)*</i>	<i>0.000453</i> <i>(0.000656)</i>	-0.0011 (0.000761)	-0.01346 <i>(0.002611)*</i>			
b) Based on manual covariates											
MODEL	Intercept	Overall	Subcanopy	Understory	Logging	Encroach	Fire-risk	Settlement	Hunting	Altitude	Slope
<i>A priori</i> relationship	NA	+	+	+	-	-	-	-	-	-	-
Best (SE)	-18.047 (1.954)	NA	NA	0.652 <i>(0.140)*</i>	NA	-0.769 <i>(0.350)*</i>	NA	-88.89 <i>(10.850)*</i>	NA	NA	0.33 <i>(0.15)*</i>
Univariate (SE)	NA	<i>-0.173</i> <i>(0.125)</i>	<i>-0.002</i> <i>(0.127)</i>	0.582 <i>(0.135)*</i>	-0.159 (0.1459)	-0.742 <i>(0.330)*</i>	-0.623 (0.352)	-160.134 <i>(7.278)*</i>	-0.198 (0.132)	0.205 (0.118)	0.359 <i>(0.127)*</i>
Average (SE)	-15.115 (5.925)	NA	NA	0.691 <i>(0.022)*</i>	NA	-0.751 <i>(0.130)*</i>	-0.019 (0.097)	-72.582 <i>(183.534)</i>	<i>0.003</i> <i>(0.004)</i>	<i>0.119</i> <i>(0.017)*</i>	<i>0.248</i> <i>(0.021)*</i>

Note: * indicates statistical significance as defined by $\hat{\beta} \pm 1.96 \times \text{SE}$; italic indicates opposite from *a priori* prediction
 AltDEM=altitude; Precip=precipitation; Dtwater=distance to freshwater; dtfedge07=distance to forest edge; dtpacr=distance to centroid of protected areas; Dtmprd=distance to major public road; dtf05cr=distance to centroid of forest block

Table 2.10. Top models ($w_i > 0$) for probability of habitat use ($\Psi_{1\text{-km}}$) by tigers based on detection history data collected at transect sites within acacia plantations ($n = 268$, at 1-km transect scale) in Central Sumatra.

a) Developed using landscape covariates					
Model	AIC	Δ AIC	w_i	Model Likelihood	K
psi(dtwater+Dtmprd),thta0,thta1,p(.)	198.15	0	0.3953	1	6
psi(dtwater+Dtmprd+Dtfedge07),thta0,thta1,p(.)	198.68	0.53	0.3033	0.7672	7
psi(dtwater),thta0,thta1,p(.)	199.15	1	0.2398	0.6065	5
psi,thta0,thta1,p(.)	205.07	6.92	0.0124	0.0314	4
psi(Dtmprd),thta0,thta1,p(.)	205.24	7.09	0.0114	0.0289	5
psi(Dtfedge07),thta0,thta1,p(.)	205.25	7.1	0.0114	0.0287	5
psi(dtpacr),thta0,thta1,p(.)	205.56	7.41	0.0097	0.0246	5
psi(dt05cr),thta0,thta1,p(.)	205.69	7.54	0.0091	0.0231	5
psi(Precip),thta0,thta1,p(.)	206.14	7.99	0.0073	0.0184	5
1 group, Constant P	212.68	14.53	0.0003	0.0007	2
b) Developed using manual covariates					
Model	AIC	Δ AIC	w_i	Model Likelihood	K
psi(Slope+subcanopy+encroach+logging), thta0,thta1,p(.)	182.66	0	0.5432	1	8
psi(Slope+subcanopy+encroach+logging+ firerisk),thta0,thta1,p(.)	183.49	0.83	0.3587	0.6603	9
psi(Slope+subcanopy+encroach),thta0,thta1,p(.)	186.29	3.63	0.09	0.1628	7
psi(Slope+subcanopy),thta0,thta1,p(.)	190.92	8.26	0.01	0.02	6
c) Developed using manual plantation-specific covariates					
Model	AIC	Δ AIC	w_i	Model Likelihood	K
psi(Age+HumanActivities+LeafLitter), thta0,thta1,p(.)	174.91	0	0.3584	1	7

psi(Age+HumanActivities+LeafLitter+ TreeHeight),thta0,thta1,p(.)	175.42	0.51	0.2777	0.7749	8
psi(Age+HumanActivities),thta0,thta1,p(.)	176	1.09	0.2078	0.5798	6
psi(Age+HumanActivities+LeafLitter+ TreeHeight+OtherPlants),thta0,thta1,p(.)	176.73	1.82	0.1443	0.4025	9
psi(Age+LeafLitter),thta0,thta1,p(.)	182.77	7.86	0.007	0.0196	6
psi(Age),thta0,thta1,p(.)	184.25	9.34	0.0034	0.0094	5
psi(LeafLitter),thta0,thta1,p(.)	186.04	11.13	0.0014	0.0038	5

Notes: Psi=probability of site occupancy/habitat use; p=probability of detection; thta0= spatial dependence parameter representing the probability that the species is present locally, given the species was not present in the previous site; thta1= spatial dependence parameter representing the probability that a species is present locally, given it was present at the previous site. Dtwater=distance to freshwater; Dtmprd=distance to major public road; dtfedge07=distance to forest edge; dtpacr=distance to centroid of protected areas; dtf05cr=distance to centroid of forest block; Precip=precipitation;

Table 2.11. Beta estimates for the logit link function for different covariates based on best model, univariate models and model average for tiger probability of habitat use ($\Psi_{1\text{-km}}$) within acacia plantations in Central Sumatra.

a) Based on landscape covariates.

MODEL	Intercept	AltDEM	Precip	Dtwater	Dtfedge07	Dtpacr	Dtmprd	dtf05cr
<i>A priori</i> relationship	NA	-	+	-	-	-	+	-
Best (SE)	-3.242085 (0.885401)	NA	NA	-1.159514 (0.441572)*	NA	NA	-0.773004 (0.440115)	NA
Univariate (SE)	NA	NA	0.347458 (0.378493)	-2.714844 (2.145005)	-0.522216 (0.456142)	-0.45453 (0.404692)	-0.55153 (0.462082)	-0.410336 (0.364662)
Average (SE)	-1.911653 (0.756066)	NA	0.000104 (0.000086)	-0.626665 (0.234392)*	-0.159413 (0.134107)	-0.00414 (0.002962)	-0.47402 (0.142732)*	-0.002995 (0.001932)

b) Based on manual covariates

Model	Intercept	Overall	Canopy	Sub-canopy	Under-story	Logging	En-croach	Fire-risk	Settle-ment	Hun-ting	Altitude	Slope
<i>A priori</i> relationship		+	+	+	+	-	-	-	-	-	-	-
Best (SE)	-59.47 (1.986)	NA	NA	1.53 (1.397)	NA	-128.65 (0.853)*	2.32 (1.43)	NA	NA	NA	NA	-2.36 (1.73)
Univariate (SE)	NA	0.46 (0.559)	0.46 (0.559)	7.33 (12.59)	0.15 (0.342)	-153.81 (1.255)*	3.25 (5.062)	-1.14 (0.89)	-32.94 (0.415)	0.43 (0.391)	0.16 (0.351)	-4.97 (4.994)
Average (SE)	-60.478 (9.406)	NA	NA	1.695 (1.817)	NA	-130.56 (50.604)*	2.089 (1.740)	-0.25 (0.365)	NA	NA	NA	-2.355 (2.644)

c) Based on plantation-specific manual covariates

MODEL	Intercept	Age	Tree Height	Husbandry	Other Plants	Leaf Litter	Human Activities	Plant Intervals	Rotation
A-priori predicted relationship	NA	+	+	-	+	+	-	+	-
Best (SE)	-8.08 (2.98)	3.26 (1.83)	NA	NA	NA	2.02 (1.35)	-3.65 (2.51)	NA	NA
Univariate (SE)	NA	7.25 (4.864)	2.74 (1.284)*	-0.97 (0.453)*	3.36 (1.725)	8.01 (5.767)	NA	-0.15 (0.314)	0.001 (0.337)
Average (SE)	-7.875 (8.144)	2.710 (3.161)	0.822 (0.848)	NA	0.083 (0.073)	1.594 (1.798)	-3.652 (5.885)	NA	NA

Note: * indicates statistical significance as defined by $\hat{\beta} \pm 1.96 \times SE$; italics indicate opposite from *a priori* prediction
 AltDEM=altitude; Precip=precipitation; Dtwater=distance to freshwater body; dtfedge07=distance to forest edge; dtpacr=distance to centroid of protected areas; Dtmprd=distance to major public road; dtf05cr=distance to centroid of forest block ;

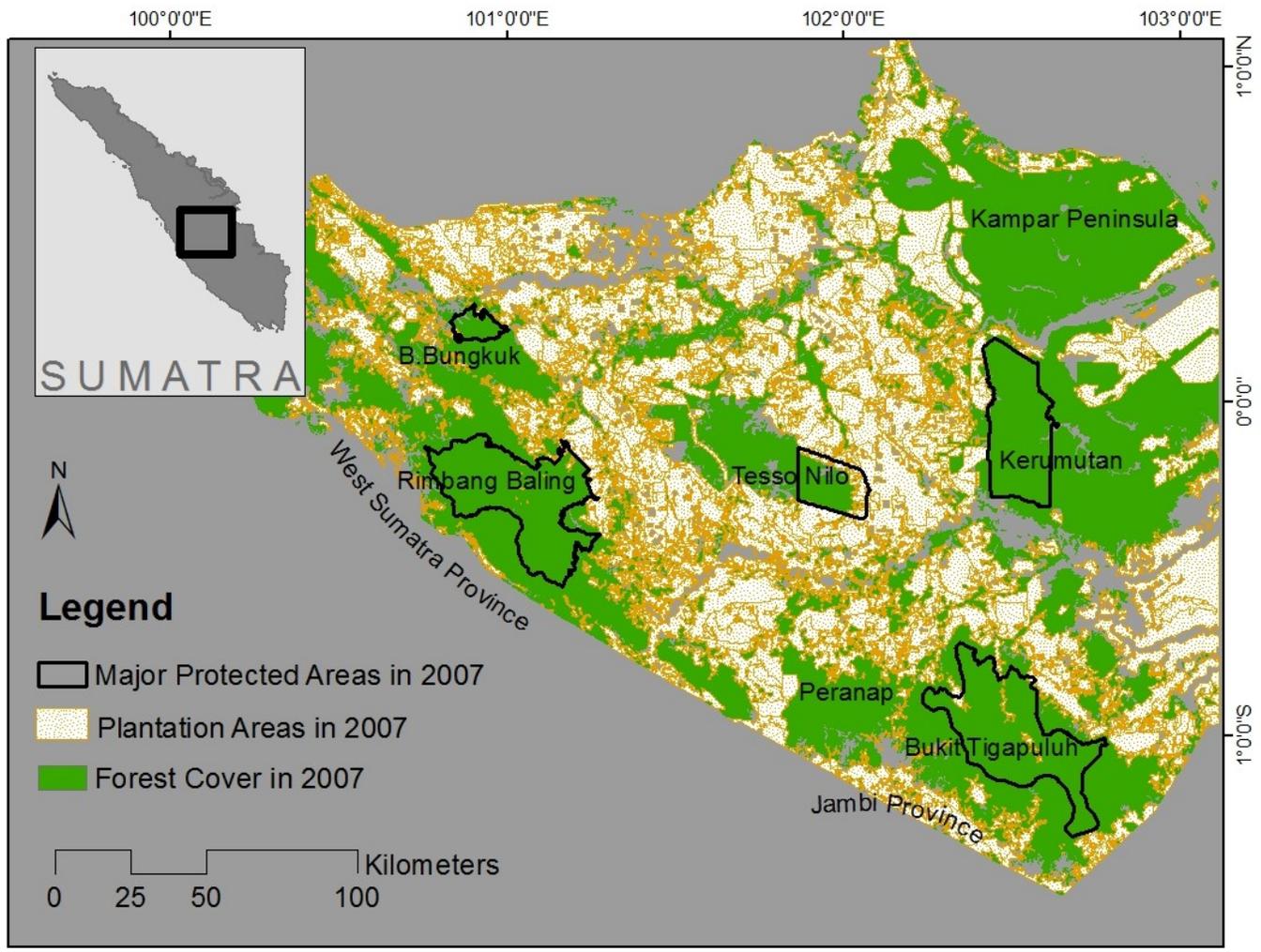


Figure 2.1. Map of the study area in central Sumatra.

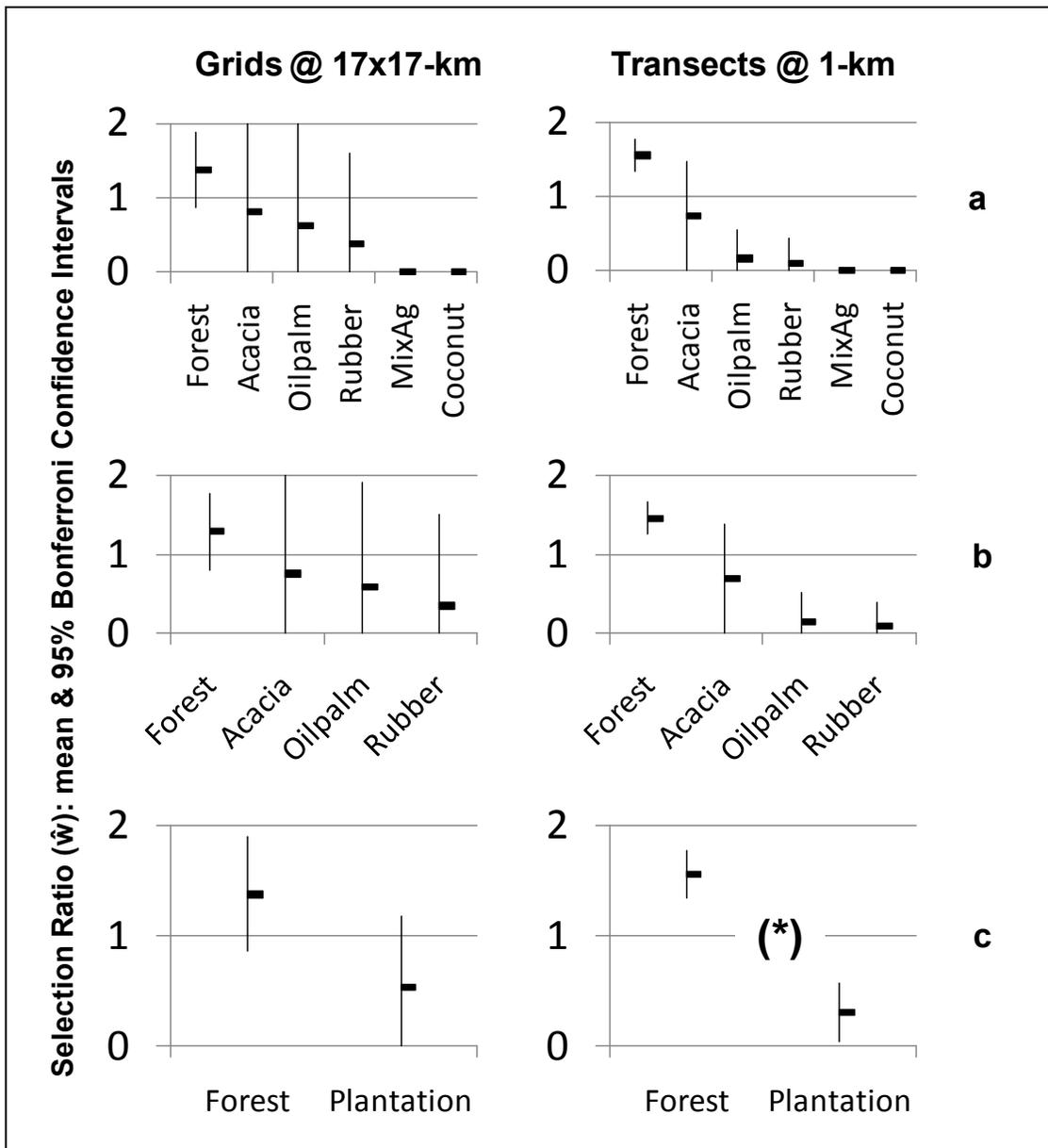


Figure 2.2. Comparison of tiger habitat selection based on 2 different sampling scales for different landcover types for a) six categories including all landcover types; b) four categories including only landcover types where tigers were detected; and c) two categories (forest vs. plantation with all plantation types combined). This analysis was conducted following the method as outlined by Manly, et al.(2004) assuming the field sampling complies with Study Design I and Sampling Protocol A. In this approach, an animal that was present or used the site was assumed to be always detected. * Denotes significant difference (from forest).

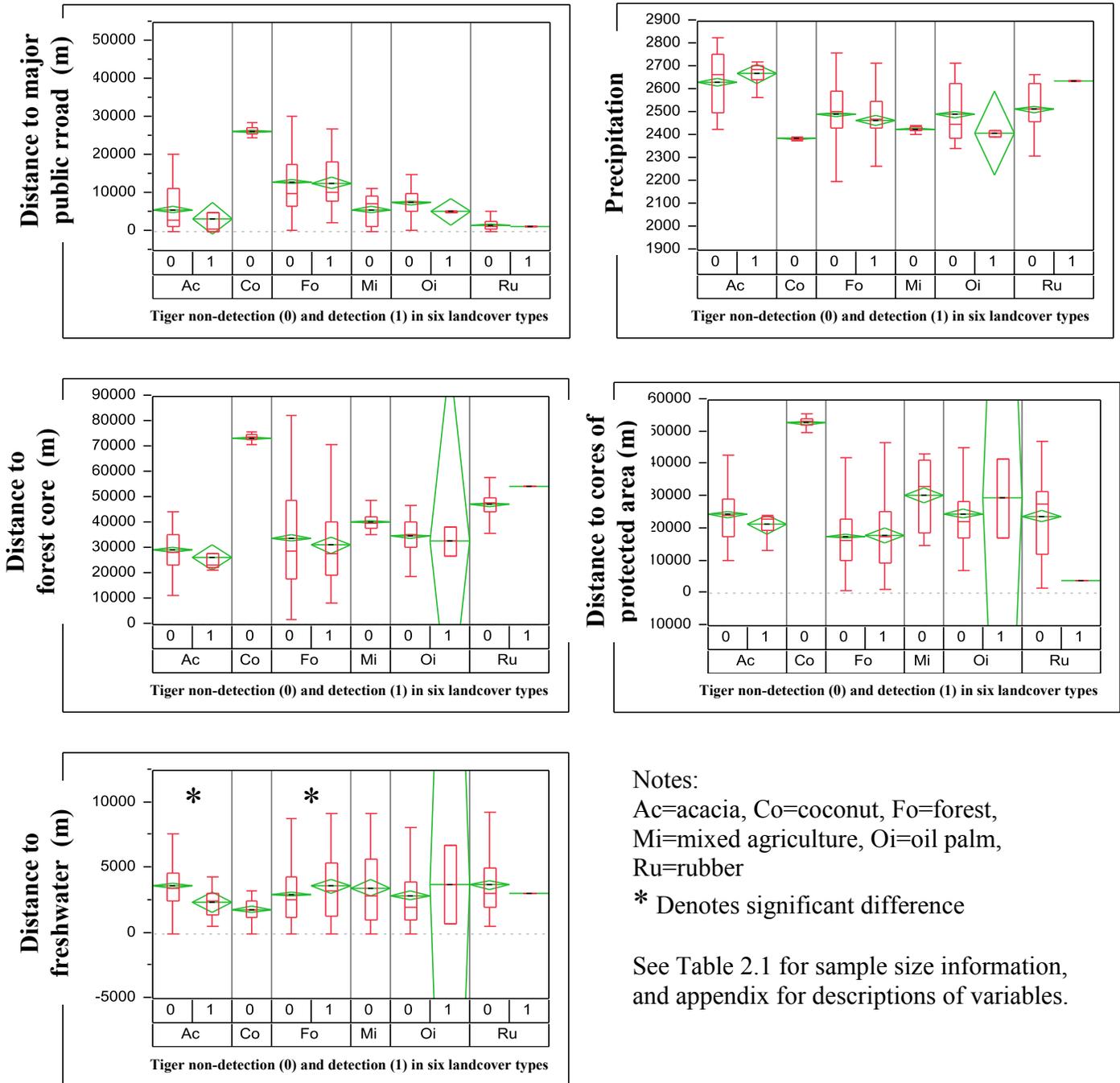


Figure 2.3. Differences in habitat conditions (based on landscape variables at 1-km transect scale) between sites where tigers were detected (1) and not detected (0) within different landcover types. Note: green diamonds show 95% Confidence Intervals. In this approach, an animal that was present, or used the site, was assumed to be always detected.

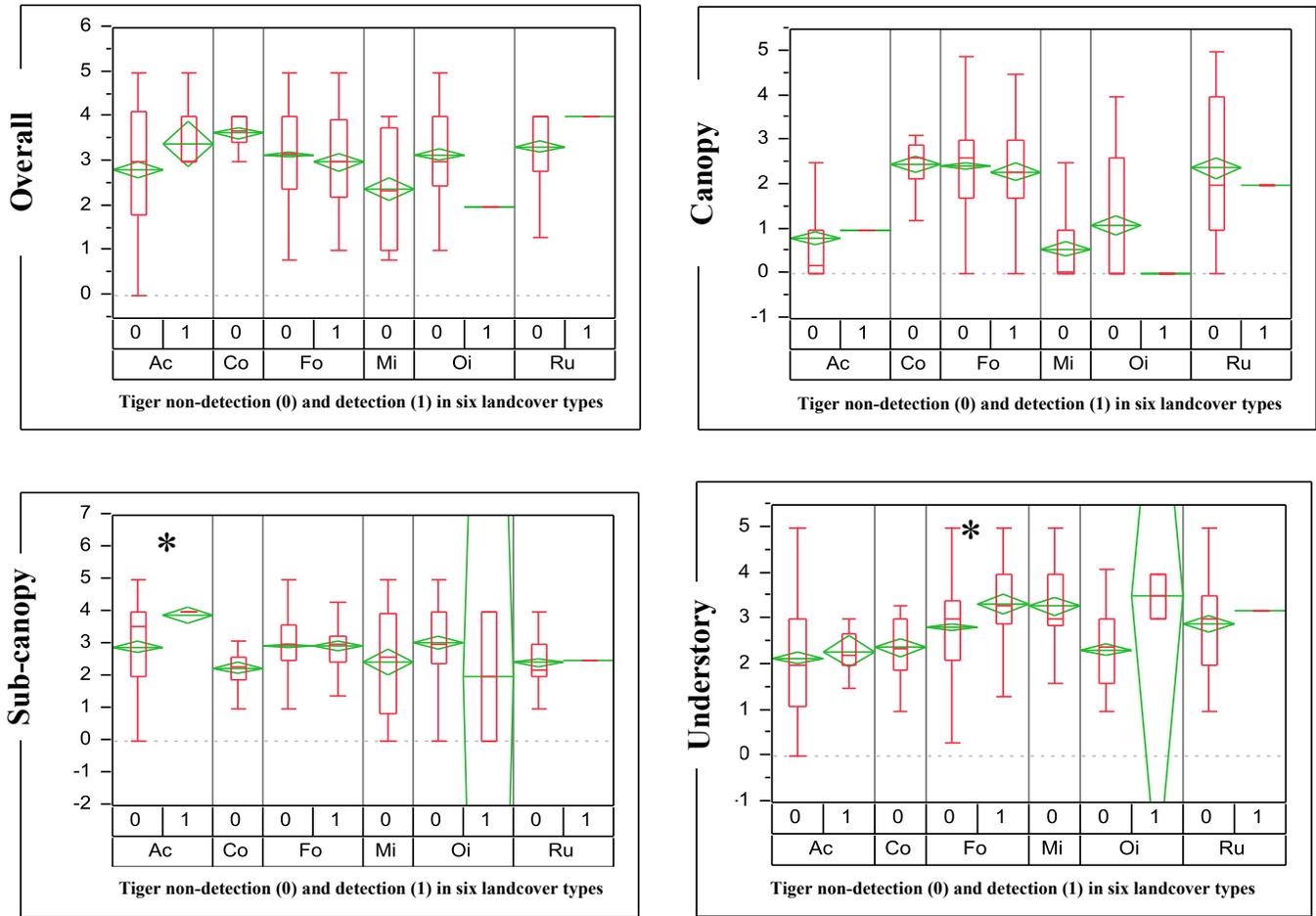
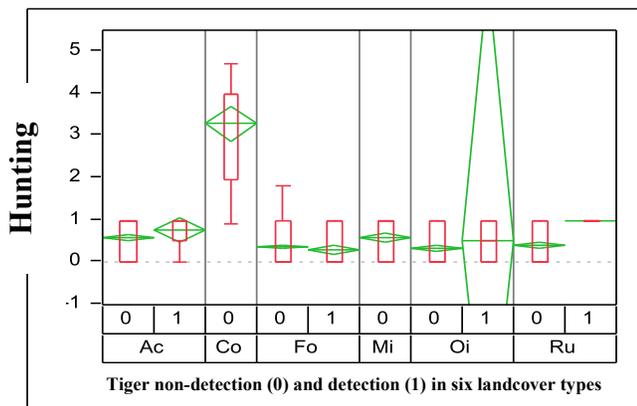
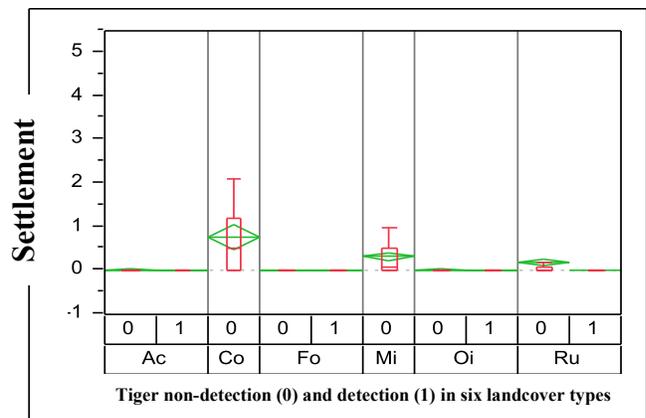
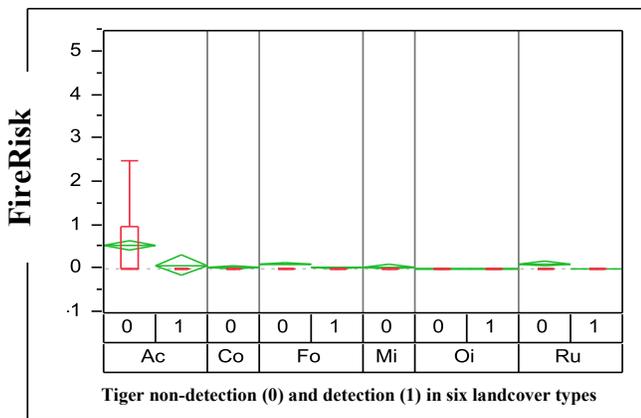
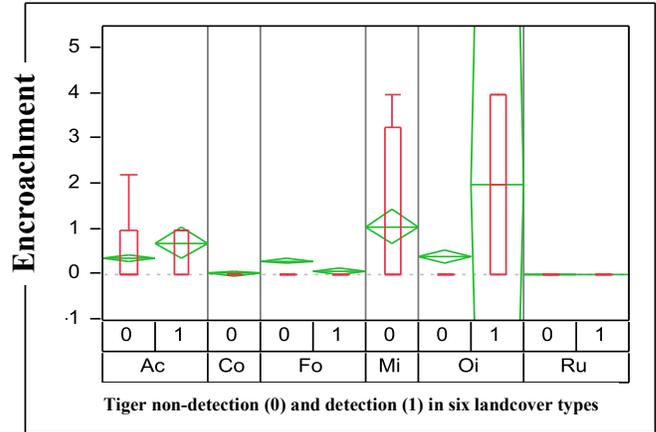
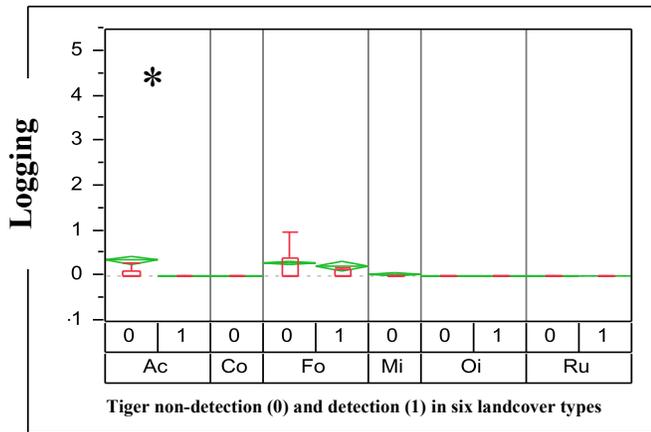


Figure 2.4a. Differences in vegetation cover (based on manual covariates measured in each 100-m segment and averaged at 1-km transect level) between sites where tigers were non-detected (0) and detected (1) within different landcover types. Note: green diamonds show 95% Confidence Intervals. In this approach, an animal that was present, or used the site, was assumed to be always detected. See Table 2.1 for sample size information, and appendix for descriptions of variables. Ac=acacia, Co=coconut, Fo=forest, Mi=mixed agriculture, Oi=oil palm, Ru=rubber. * Denotes significant difference.



Notes:

Ac=acacia, Co=coconut, Fo=forest, Mi=mixed agriculture, Oi=oil palm, Ru=rubber

* Denotes significant difference

Green diamonds show 95% Confidence Intervals. In this approach, an animal that was present, or used the site, was assumed to always be detected. See Table 2.1 for sample size information, and appendix for descriptions of variables.

Figure 2.4b. Differences in disturbance level (based on manual covariates measured in each 100-m segment and averaged at 1-km transect level) between sites where tigers were not-detected (0) and detected (1) within different landcover types.

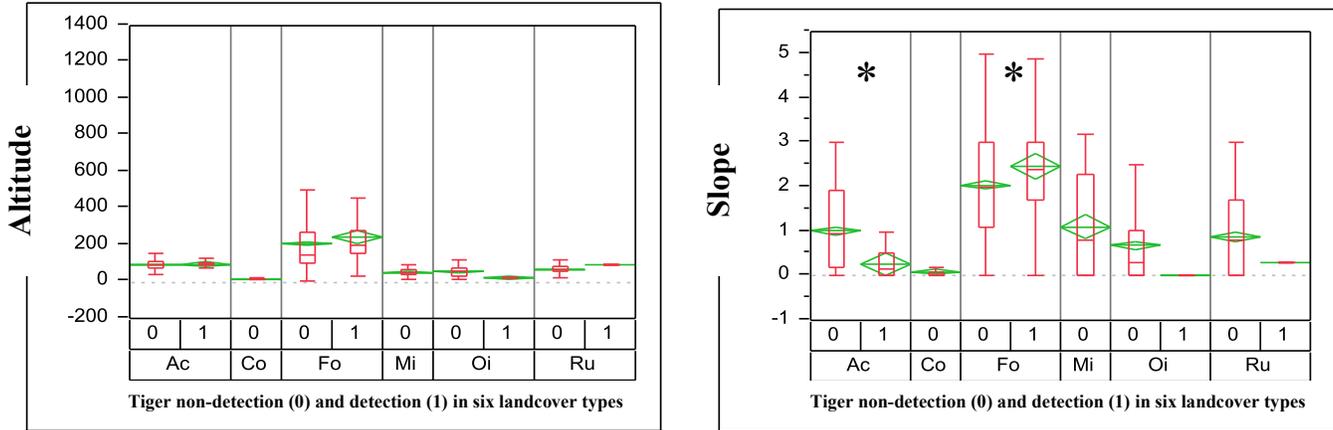


Figure 2.4c. Differences in terrain condition (based on manual covariates measured in each 100-m segment and averaged at 1-km transect level) between sites where tigers were non-detected (0) and detected (1) within different landcover types. Note: green diamonds show 95% Confidence Intervals. In this approach, an animal that was present or used the site, was assumed to always be detected. See Table 2.1 for sample size information, and appendix for descriptions of variables. Ac=acacia, Co=coconut, Fo=forest, Mi=mixed agriculture, Oi=oil palm, Ru=rubber; * Denotes significant difference.

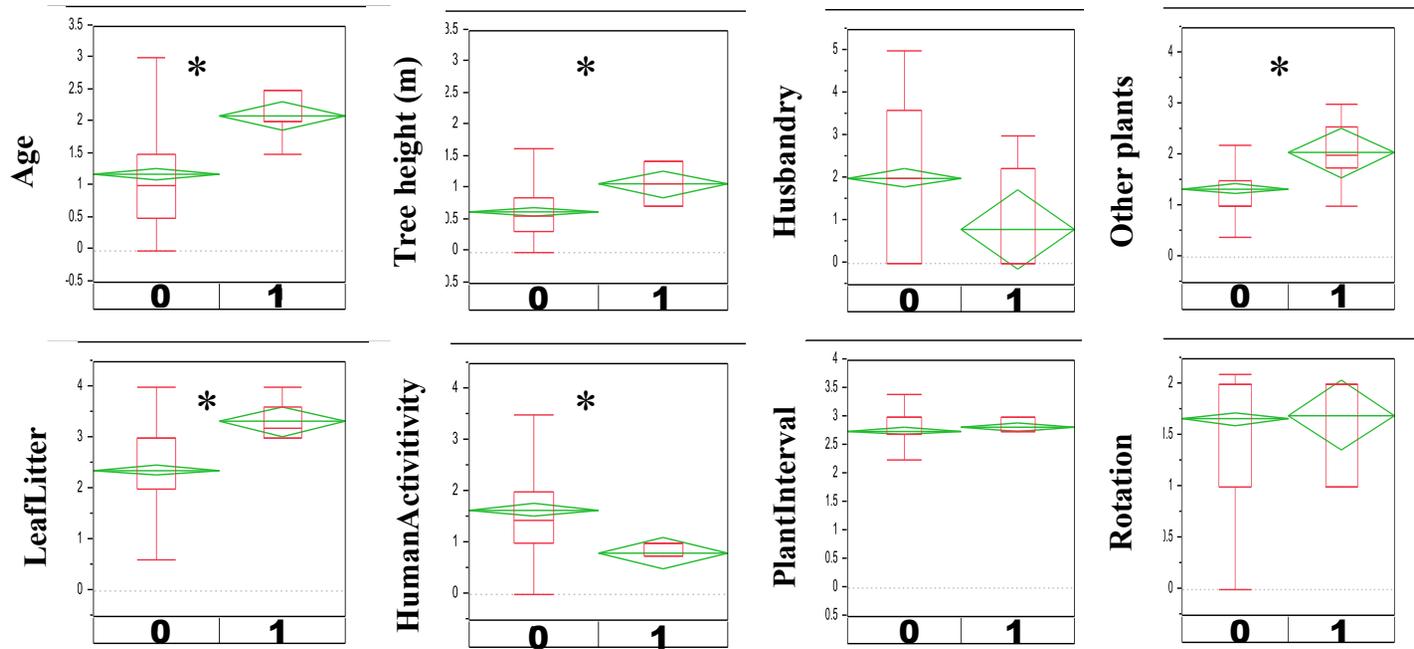


Figure 2.5a. Comparison of plantation characteristics between acacia plantation sites (based on manual covariates measured in each 100-m segment and averaged at 1-km transect level) where tigers were not detected (0) and detected (1). Note: green diamonds show 95% Confidence Intervals. In this approach, an animal that was present, or used the site, was assumed to always be detected. See Table 2.1 for sample size information, and appendix for descriptions of variables. * Denotes significant difference.

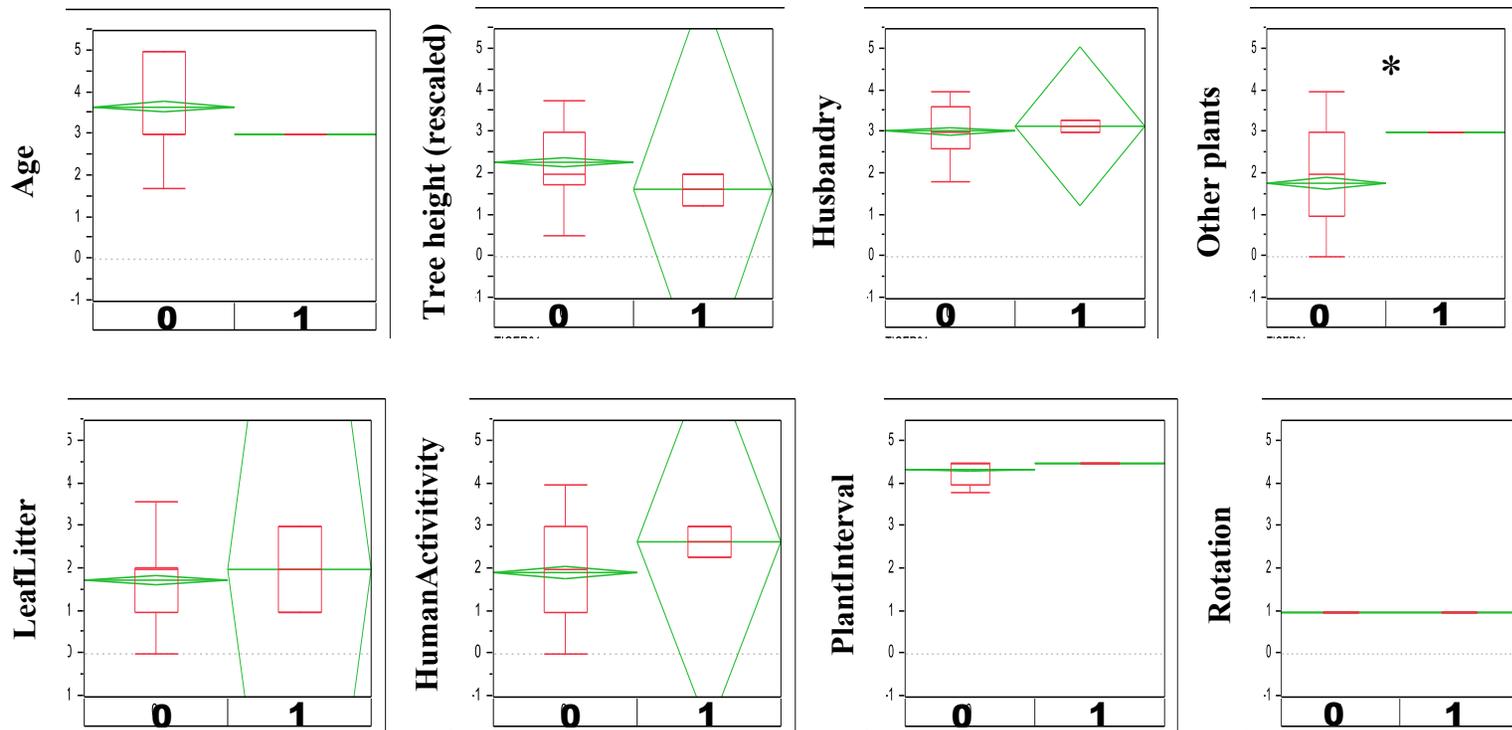


Figure 2.5b. Comparison of oilpalm plantation characteristics (based on manual covariates measured in each 100-m segment and averaged at 1-km transect level) between sites where tigers were not detected (0) and detected (1). In this approach, an animal that was present, or used the site, was assumed to always be detected. See Table 2.1 for sample size information. * Denotes significant difference.

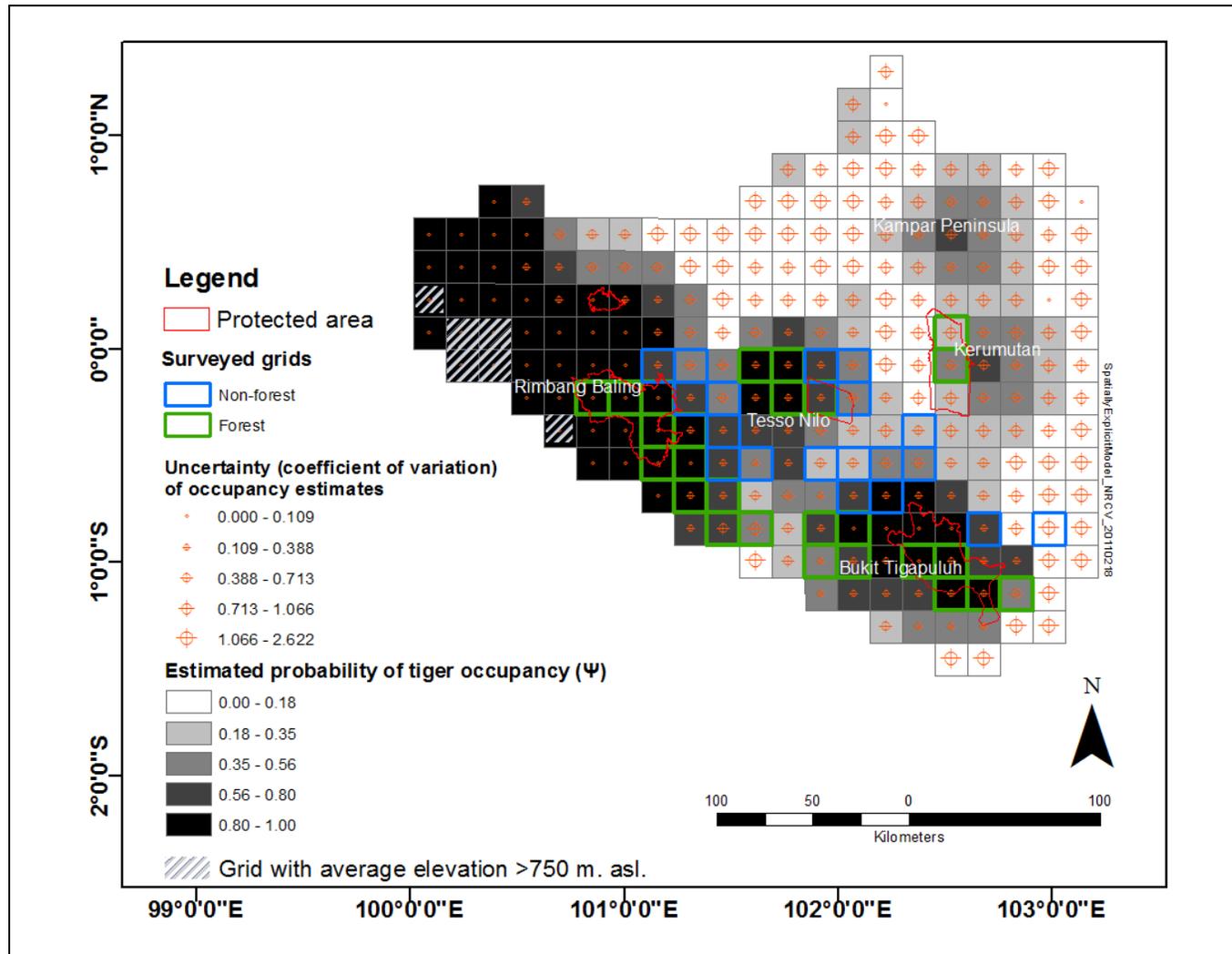


Figure 2.6. Map of probability of tiger occupancy in the central Sumatra landscape constructed from the best occupancy model developed based on the landscape-scale survey in 17x17 km grid cells representing forest and other major landcover types.

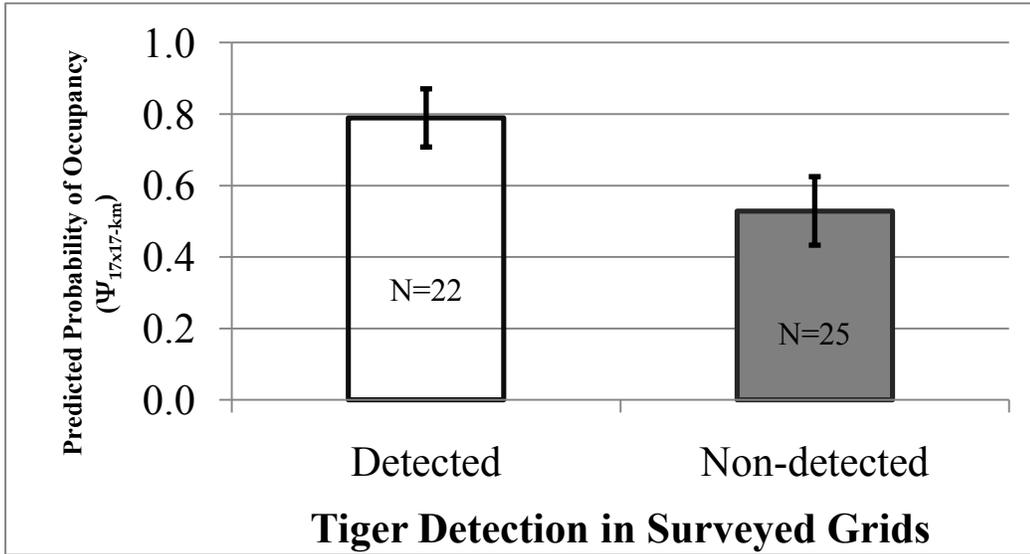


Figure 2.7. Comparisons of predicted probability of occupancy ($\Psi_{17 \times 17\text{-km}}$) between grids where tigers were detected and non-detected during surveys based on data used to develop the landscape-scale tiger occupancy models (Bars indicate 95% confidence limits).

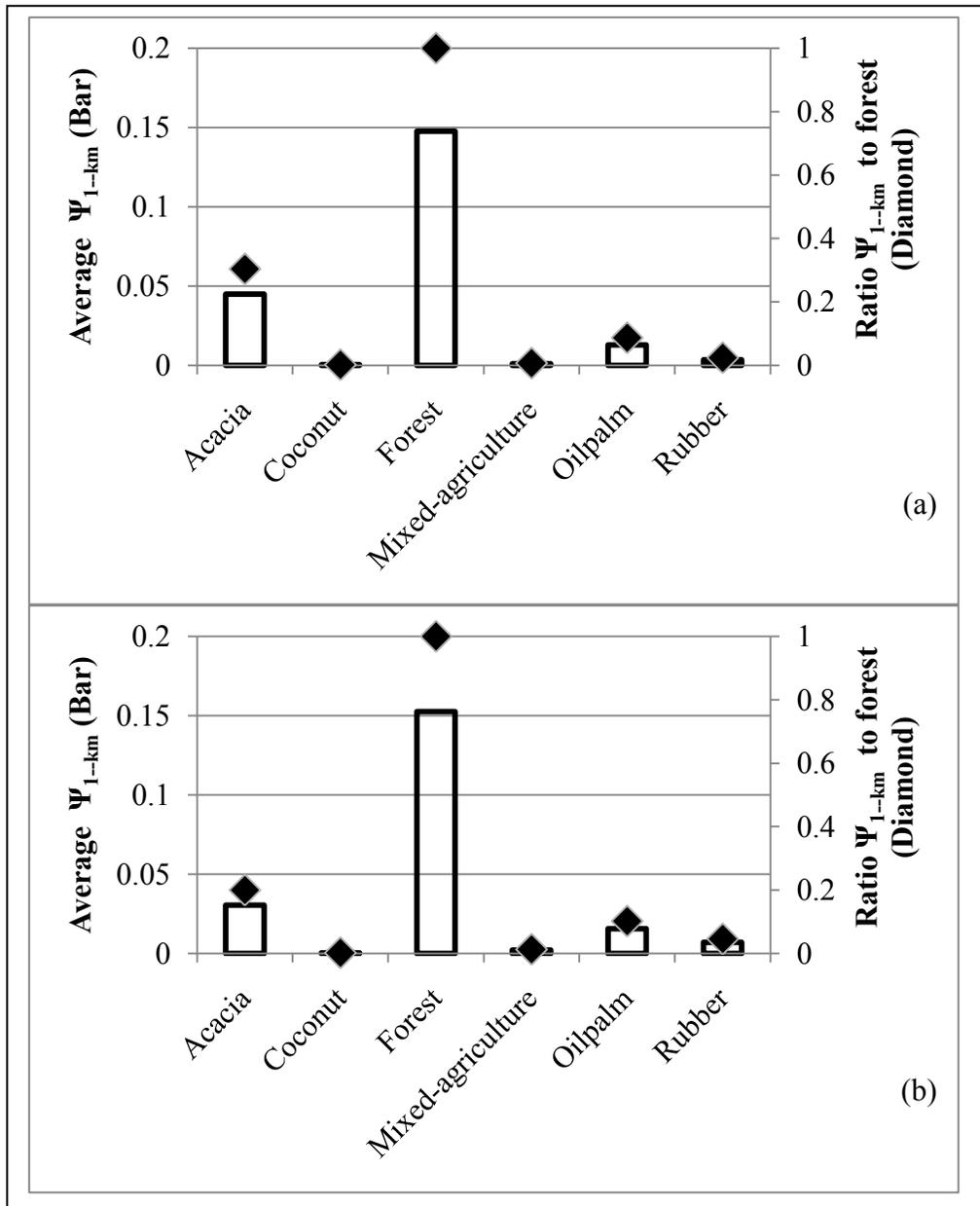


Figure 2.8. Estimated probability of habitat use (Ψ_{1-km}) from the best model for each landcover (bars) and ratio of plantation's probability of use (diamonds) relative to forest based on a) landscape covariates and b) manual covariates.

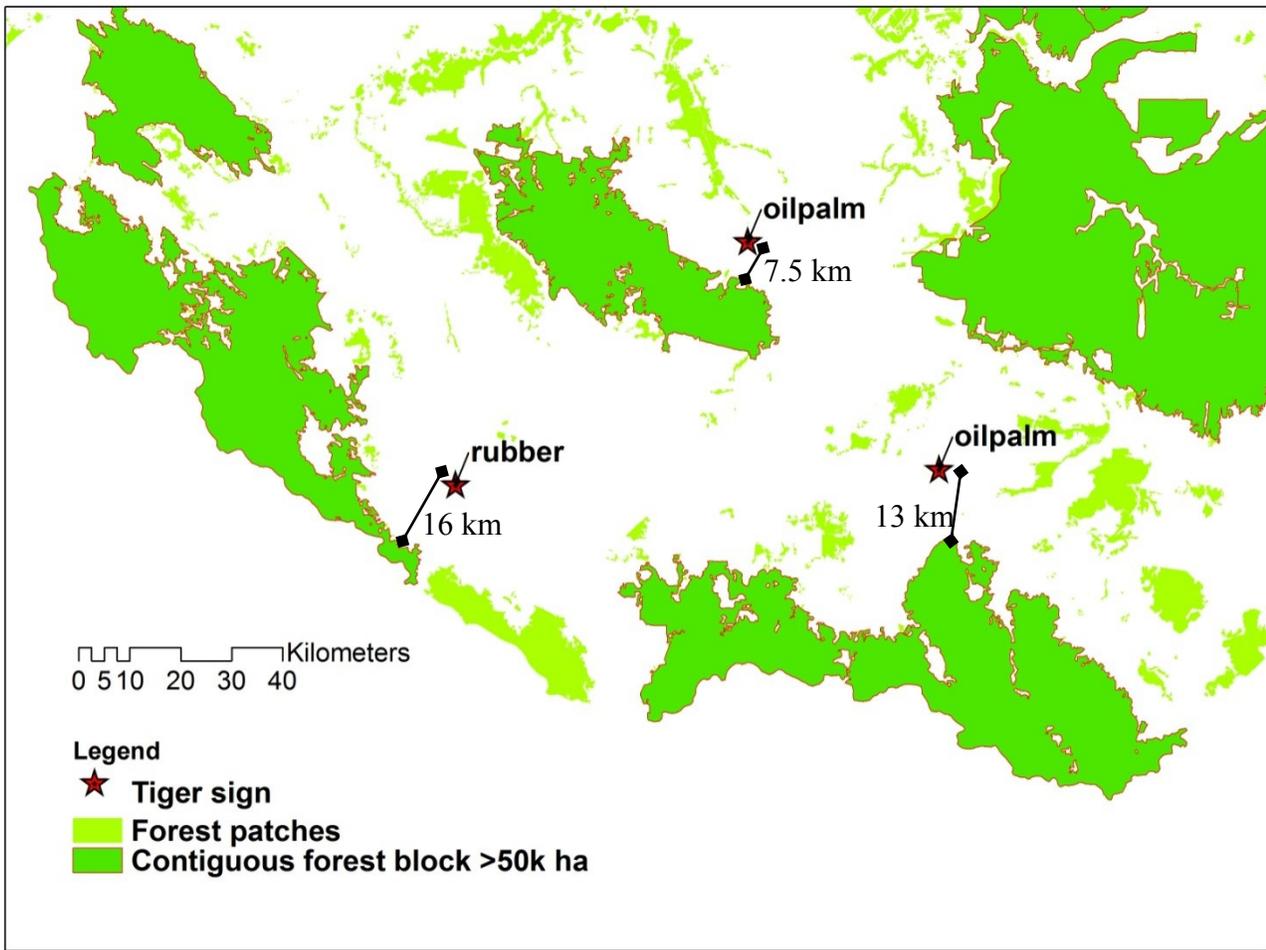


Figure 2.9. Locations of tiger sign found in oilpalm and rubber plantations relative to main forest blocks and forest patches in Central Sumatra.

Appendix 2.1a. List of habitat and environmental variables (manual covariates) collected in every 100-m segment along transects.

Variable Name	Description & scale of measurement
TERRAIN	
Alt	Altitude or elevation in meter based on reading from GPS' barometric altimeter
Slope	The level of slope: 0=flat to 5=very steep
VEGETATION COVER	
habdom	General coverage condition of the vegetation (0=very open to 5=very dense/close)
canopy	Coverage of canopy (>30 cm diameter trees): 0 = 0%, 1 = 1-20 %, 2 = 21-40%, 3 = 41-60 %, 4 = 61-80 %, 5 = 81-100 %
subcanopy	Coverage of sub-canopy (sapling and trees<30cm): 0 = 0%, 1 = 1-20 %, 2 = 21-40%, 3 = 41-60 %, 4 = 61-80 %, 5 = 81-100 %
ground	Ground cover (seedlings and herbaceous plants): 0 = 0%, 1 = 1-20 %, 2 = 21-40%, 3 = 41-60 %, 4 = 61-80 %, 5 = 81-100 %
lccode	Ordinal coding of landcover types assigned based on general impression on its relationship/distance (e.g., geographically, historically) to forest: forest=1, acacia=2, oilpalm=3, rubber=4, mix agriculture=5, coconut=6
DISTURBANCE	
logging	The level of disturbance from logging activities: 0=none to 5=very high
encroach	The level of disturbance from encroachment activities: 0=none to 5=very high
fire	The level of disturbance from, or risk of fires: 0=none to 5=very high
settlement	The level of disturbance from settlement: 0=none to 5=very high
hunting	The level of disturbance from, or risk of hunting activities: 0=none to 5=very high

Appendix 2.1b. Additional environmental variables (manual plantation-specific covariates) collected in every 100-m segment along transects in plantation areas.

Variable Name	Description	Scale of Measurement
Age	Age of the plantation	Scores of 0 to 5
Height	Height of the plantation	meter
Husbandry	The intensity of plantation husbandry or maintenance	Scores of 0 to 5
Otherplant	The density of plants other than the main commodities	Scores of 0 to 5
Leaf litter	The coverage of leaf litter	Scores of 0 to 5
Humanact	The intensity of human activities	Scores of 0 to 5
Plantint	Space interval between plants of the main commodity species	Meter
Rotation	The rotation of plant since the area was opened from natural forest or other landcover types	Number

Appendix 2.1c. List of landscape variable derived from GIS, the original source, and treatments to the data.

No	Variable	Original Source	Treatment & Range of Values
1	<i>Distance to major public road</i> ("DtMPRd")	<i>Road data from Indonesian National Mapping Agency (BAKOSURTANAL)</i>	<i>The original data were corrected for known errors. Distance to road raster data were derived using FindDistance in ArcView 3.2. Values range from 0 to 96,112 (\bar{x} = 15,641) meter.</i>
2	<i>Distance to centroid forest area</i> ("dtf05cr")	<i>Forest-non forest classification done by WWF (Setiabudi 2006) based on satellite images (spatial resolution ~30 m) acquired in 2005</i>	<i>Forest blocks were defined as contiguous forest area equal to or greater than 50,000 ha. Centroids of forest blocks were determined using 'Generate Polygon centroid point' in Hawth's Analysis Tools Version 3.27 (www.spatialecology.com). Distance to the Forest centroid raster data were derived using FindDistance in ArcView 3.2. Spatial Analyst. Values range from 7810 to 94032 (\bar{x} = 41642) meter.</i>
3	<i>Distance to forest edge</i> ("Dtfedge07")	<i>Forest-non forest classification done by WWF (Setiabudi 2006) based on satellite images (spatial resolution ~30 m) acquired in 2007</i>	<i>Using XTools version 6/1/2001 extension in ArcView 3.2, convert forest polygons to polylines (forest edge). Distance to the Forest edge raster data were derived using FindDistance in ArcView 3.2. Spatial Analyst. Values range from 0 to 47,539 (\bar{x} = 7,024) meter.</i>
4	<i>Distance to centroid of protected areas</i> ("Dtpacr")	<i>Protected area map was available from Indonesian Ministry of Forestry, maintained and updated by WWF Indonesia GIS team</i>	<i>Centroids of protected areas were determined using 'Generate polygon centroid point' in Hawth's Analysis Tools Version 3.27 (www.spatialecology.com). Distance to the Forest centroid raster data were derived using FindDistance in ArcView 3.2. Spatial Analyst. Values range from 2236 to 81844 (\bar{x} = 31,035) meter.</i>
5	<i>Precipitation</i> ("Precip")	<i>Bioclim interpolated precipitation version 1.4 Release 3. Spatial resolution of 30 arc-second (~ 1 square km), http://www.worldclim.org/ (Hijmans et al. 2005),</i>	<i>Total annual precipitation (using raster calculator in spatial analyst, sum of 12 months' precipitation from the original data). Data for the study area were clipped using SpatialAnalyst>Extraction>Extract by Mask. Values range from 1989 to 2830 (\bar{x} = 2509) mm.</i>

No	Variable	Original Source	Treatment & Range of Values
6	<i>Distance to freshwater</i> (“Dtwater”)	Rivers, canals, and lakes data as separate files from Digital Chart of the World Vector (line and area), downloaded through http://www.diva-gis.org/gData	Separate files were combined into one feature file in ArcGIS 9.3.1. and distance to the freshwater raster data were derived using FindDistance in ArcView 3.2. Values range from 0 to 11,677 (\bar{x} = 3,176) meter.
7	<i>Altitude</i> (“AltDEM”)	CIAT DEM SRTM (Shuttle Radar Topographic Mission) <i>version 4</i> . http://srtm.csi.cgiar.org/index.asp CIAT: International Center for Tropical Agriculture. These data were originally derived from USGS/NASA SRTM data (Jarvis et al. 2004), resampled to 250 m resolution.	No treatment. Values range from 1 to 910 (\bar{x} = 139) meter.
8	<i>Slope</i> (“Slope”)	<i>Derived from DEM SRTM version 4</i> 250 m resolution http://srtm.csi.cgiar.org/index.asp , (Jarvis et al. 2004)	<i>Slopes (in percent) were derived from DEM SRTM in ArcGIS 9.3.1. using Spatial Analyst Tools.</i> Values range from 0 to 22 (\bar{x} = 1.4) percent.
9	<i>Distance to Deforestation 06 to 07</i> (“Dtdef0607”)	<i>Forest-non forest classification</i> available from a series of years: 1982, 1988, 1996, 2000, 2002, 2004, 2005, 2006, 2007 (Uryu et al. 2007).	Deforestation or forest loss were calculated using forest cover layers from two different years (2006 and 2007, the available layers closest to the time of survey). Deforested areas were identified using Erase function in ET GeoWizard. Values range from 0 to 26,019 (\bar{x} = 7196) meter.
10	<i>Forest area 07</i> (“For07Area”)	<i>Forest-non forest classification</i> (Uryu et al. 2007)	Forest area within each grid cell was calculated using <i>Hawth's Analysis Tools Version 3.27</i> (www.spatial ecology.com). Values range from 0 to 288,090,761 (\bar{x} = 72,811,383) m ² .

Appendix 2.2a. Pearson Correlation between landscape variables for grid level (17x17 km)

	<i>Def0607</i>	<i>For07Area</i>	<i>AltDEM</i>	<i>dtf05cr</i>	<i>dtpacr</i>	<i>Dtmprd</i>	<i>Precip</i>
<i>Def0607</i>	1.00						
<i>For07Area</i>	0.22	1.00					
<i>AltDEM</i>	0.03	0.07	1.00				
<i>dtf05cr</i>	-0.23	-0.56	-0.07	1.00			
<i>dtpacr</i>	0.04	-0.37	-0.02	0.61	1.00		
<i>Dtmprd</i>	0.10	0.25	-0.27	-0.01	0.01	1.00	
<i>Precip</i>	-0.13	-0.06	0.47	0.09	0.09	-0.40	1.00

Note: *Dtdef0607*=Distance to deforested area 06 to 07, *For07Area*= Forest area 07, *AltDEM*=altitude, *dtf05cr*= Distance to centroid forest area, *Dtpacr*= Distance to centroid of protected areas, *Dtmprd*=Distance to major public road, *Precip*=precipitation

Appendix 2.2b. Pearson Correlation between landscape variables for transect level (extracted from 500 meter buffer around start- and end-point of each 1-km transect).

	dtmprd	precip	dtfedge07	dtdef0607	dtf05cr	dtpacr	dtwater	altDEM	slope
dtmprd	1.00								
precip	-0.39	1.00							
dtfedge07	-0.04	-0.05	1.00						
dtdef0607	0.15	-0.27	0.60	1.00					
dtf05cr	0.08	0.08	0.37	0.26	1.00				
dtpacr	-0.11	-0.03	0.24	0.23	0.27	1.00			
dtwater	-0.09	-0.14	0.04	0.09	0.03	0.15	1.00		
altDEM	0.01	-0.25	-0.09	0.21	0.00	-0.26	0.03	1.00	
slope	0.10	-0.37	-0.08	0.18	-0.01	-0.19	0.05	0.81	1.00

Note: Dtmprd=Distance to major public road, Precip=precipitation, Dtfedge07=distance to forest edge, Dtdef0607=Distance to deforested area 06 to 07, dtf05cr= Distance to centroid forest area, Dtpacr= Distance to centroid of protected areas, dtwater= distance to freshwater, AltDEM=altitude, slope=slope

Appendix 2.2c. Pearson correlation for manual covariates

	overall	canopy	Sub- canopy	Under- story	logging	Encro- achment	Fire- risk	Settle- ment	hunting	slope
overall	1.00									
canopy	0.45	1.00								
subcanopy	0.34	0.00	1.00							
understory	-0.07	0.08	-0.04	1.00						
logging	-0.13	-0.10	-0.14	-0.06	1.00					
encroachment	-0.38	-0.31	-0.28	0.01	0.31	1.00				
firerisk	-0.02	-0.24	-0.18	-0.09	0.35	0.26	1.00			
settlement	-0.03	-0.02	-0.12	0.03	-0.01	0.10	0.07	1.00		
hunting	0.10	-0.07	-0.07	-0.02	0.20	0.23	0.21	0.33	1.00	
slope	0.07	0.30	0.17	0.11	0.03	0.01	-0.16	-0.13	-0.10	1.00
alt	0.21	0.33	0.12	-0.14	0.04	-0.11	-0.07	-0.15	-0.11	0.57

Appendix 2.2d. Correlation coefficients for manual plantation-specific covariates

	<i>Age</i>	<i>Tree- Height</i>	<i>Hus- bandry</i>	<i>Other- Plants</i>	<i>Leaf- Litter</i>	<i>Human- Activities</i>	<i>Plan- Intervals</i>
Age	1						
TreeHeight	0.54	1					
Husbandry	-0.26	-0.09	1				
OtherPlants	0.40	0.26	-0.38	1			
LeafLitter	0.59	0.29	-0.12	0.12	1		
HumanActivities	-0.08	0.14	-0.03	-0.18	-0.17	1	
PlanIntervals	0.09	-0.14	0.03	0.01	0.05	-0.23	1
Rotation	0.14	0.22	0.29	-0.35	0.33	0.28	-0.29

Chapter 3

Wild felids in Central Sumatra: their ecological characteristics, interactions, and the implications for management

ABSTRACT

At least six species of wild felids are present in Sumatra and most of them are globally threatened. Ecological characteristics of these species are poorly known and, except for the Sumatran tiger, the other five species have barely been studied. I investigated the ecological characteristics and possible inter-specific interactions among the wild felids in Central Sumatra based on data collected using systematic camera trapping in combination with information from the literature. My team and I conducted camera trapping in five sampling blocks (each ~160 km²) representing three major forest types (peatland forest, flat dry lowland forest, and hilly forest). We placed each of 104 camera trap stations within a different 2x2 km grid cell and accumulated 7,513 effective trap nights in total. We also collected an additional 5,315 effective trap nights from *ad hoc* placements. Using felid detection, non-detection data from camera traps to estimate species presence (the response variables), I developed habitat models within the occupancy framework run in Program PRESENCE. I assessed the probability of habitat/site use by different felids based on: landscape-level factors extracted with Geographic Information System software and site-level factors in the forms of level of activity/photo-trap rates of other species documented from the same camera units. Species interactions were investigated using two approaches: a) two-species occupancy models run in Program PRESENCE to assess the spatial overlap and b) kernel density estimate (KDE) on circular data run in R software to assess the level of activity/temporal overlap between species. My team and I photographed five species of felids: Sumatran tigers, Sundaland clouded leopards, Asiatic golden cats, marbled cats, and leopard cats. Based on their life histories and morphological characteristics, I found that despite overlap in resource needs, each species appears adapted to specific environmental conditions allowing them to coexist with other felids. Spatially, their distributions varied among the different major forest blocks, within the sampling blocks, and across the elevation range. The five felids used different elevations, with the golden cat found to inhabit the highest elevation. Three felids were present in all sampling blocks, while there was only one sampling block where all five felids were photographed. Based on the landscape factors I found that the presence (probability of site use) of tigers and/or leopard cats negatively covaried with distance to protected areas. Tiger presence also negatively covaried with distance to major public roads. Clouded leopard presence positively covaried with altitude. Models incorporating site-level factors revealed that the presence of leopard cats significantly covaried positively with the photo-trap rate of Sumatran tigers, while the presence of tigers covaried with the photo-trap rate of non-felid carnivores. Two-species occupancy models showed that all possible pairs of felid species tended to co-occur more frequently than expected by chance, indicating the tendency of every felid pair to maintain spatial coexistence rather than exclusion. Consistent with the literature, KDE models revealed that tigers and leopard cats did not differ in their daily activity patterns. Species of similar size, or with similar sized prey, generally had low coefficients of temporal

activity overlap, suggesting avoidance. Temporal avoidance is likely occurring in three pairs of felids: clouded leopards and golden cats, clouded leopards and marbled cats, and marbled cats and leopard cats. Based on the differences in morphological and ecological characteristics, and patterns of spatial and temporal occurrence revealed from this study, I identified six possible mechanisms by which felids in Central Sumatra maintain coexistence. I discuss the implications of this study for management, focusing on how to balance diversity and abundance of felids.

Keywords: *Catopuma*, *Felis*, competition, *Neofelis*, *Panthera*, *Prionailurus*, inter-specific interaction, resource/niche partitioning, Sumatran tigers, sympatric carnivores, wild cat community

INTRODUCTION

Sumatra maintains rich mammal diversity which includes not only well known Asian charismatic megafauna such as the orangutan, rhino, and elephant, but also many carnivores, especially wild felids. Seven out of nine living wild felid species known to be distributed in Indonesia have been recorded in Sumatra (Nowell and Jackson 1996). For comparison, the neighboring island of Borneo which is larger in size has only five; while Java, after losing the Javan tiger, currently has only three wild felid species remaining. There are no wild felids recorded to the east beyond the islands of Borneo or Bali. This paper describes ecological characteristics, investigates inter-specific interactions, and discusses management implications of findings for the wild felids in Central Sumatra.

The extreme scarcity of information on Sumatran wild felids hampers their effective conservation. Except for the Sumatran tiger *Panthera tigris sumatrae*, there is little field study or information available on the natural history or ecological characteristics of most other wild felids in Sumatra. The information that does exist is mostly from anecdotal records of felid detection, mainly from sign observed in an *ad hoc* manner. Introductory study on felid distribution and abundance has been done for Sundaland clouded leopard *Neofelis diardi* (Santiapillai and Ashby 1988, Santiapillai 1989, Hutajulu et al. 2007), and radio collaring has recently been initiated for Asiatic golden cats *Catopuma temmincki* (Jennifer McCarty, *pers.*

comm.). For all other species, however, information is limited to occurrence data which are simply species lists of animals in management plans of certain protected areas (e.g., Ministry of Forestry 2006), within databases pertinent to certain areas of interest such as endemic bird areas (e.g., Holmes and Rombang (2001)), or, less commonly, reported specifically after sightings or investigations (e.g., Bezuijen 2000, Wibisono and Mccarthy 2010). We lack even fundamental knowledge of species presence. For example, it is unknown whether the fishing cat *Prionailurus viverrinus* occurs in Sumatra (Melisch et al. 1996, Duckworth et al. 2009, Sanderson 2009). The gap in such fundamental information must be filled for effective conservation to take place.

The high rate of forest loss and degradation of natural habitats taking place on the island makes the requirement for obtaining natural history and ecological information extremely urgent if wild felids are to be effectively conserved in Sumatra. Thanks to the relatively active tiger research and tiger conservation projects, information on other wild cats is becoming available through tiger camera trapping studies. This paper represents such a study where the documentation of felid community data results from an integrated study to reveal the ecology of tigers, their prey, and other sympatric carnivores.

Occurring together and interacting with each other, several species form a community, whose characteristics are the result of the properties of each species (Pielou 1974). Understanding the role of inter-specific competition and resource partitioning, which are important processes shaping community structure, will enhance effective management of this wildlife community. For example, the Sumatran felid community appears to consist of competing sympatric species with similar resource requirements. Therefore, this should result in resource use or niche separation, which can determine the distribution or composition of animal communities (Connell 1961). I used data from camera traps systematically placed across five

study sites representing three major forest types (peat land forest, flat dry lowland forest, and hilly forest), as well as *ad hoc* placement of cameras across the landscape to determine the extent of ecological niche partitioning and to investigate possible interactions among wild felids in Central Sumatra.

In this study, I determined 1) general ecological characteristics of each species and separation among five species in relation to geographical location and altitude, 2) factors affecting the probability of site/habitat use by every felid species, 3) the interaction between felid species as indicated by the level of co-occurrence, spatially and temporally. Finally, I discuss management implications of findings from this study.

STUDY AREA

This study took place in the southern Riau landscape, Central Sumatra (Figure 3.1). Zoo-geographically, it is located within the Kampar-Batanghari region (Whitten et al. 2000). The conservation landscape includes four major protected areas: Rimbang Baling Wildlife Reserve (RBWR), Tesso Nilo National Park (TNNP), Bukit Tigapuluh National Park (BTNP), and Kerumutan Wildlife Reserve (KRWR).

Types of natural forest in the landscape vary from peat swamp such as in the Kerumutan and Kampar Peninsula, to dry and relatively flat lowland forest as in Tesso Nilo, and hilly forest in Rimbang Baling and Bukit Tigapuluh. More detailed accounts about these areas are available in Sunarto et al. (2008).

Depending on the location, other forests are mainly under the status of “Protection Forest” (mainly for the protection of watershed) or (ex-) logging concessions which mostly are allocated for industrial plantation concessions. The “Protection Forests” generally lie in higher altitudes and steeper terrain or in peat swamp lands, while the logging concessions typically

cover relatively flat lowland areas. Non-forested lands in the landscape mainly consist of acacia and oil palm plantations. In smaller proportion, there were also mixed-agriculture, rubber plantations, and a few other landcover types (Setiabudi 2006). The landscape covers a total area of ca. 30,000 km².

There are five major forest blocks in the landscape, each separated by non-forest areas. Natural forest connectivity generally remains between BTNP and RBWR, where Bukit Sosa Protection Forest and Bukit Betabuh Protection Forest extend beyond the two larger conservation areas. This forest connectivity is by no means completely intact. Public roads and plantations interrupt the connectivity in several places. Meanwhile, land conversion by both small farmers and large agricultural/forestry companies are underway.

Overall, the study area has high precipitation ranging between 2000 and 3000 mm annually, and high humidity (above 80%). From 2004 to 2006, a local weather station recorded the average annual rainfall of 2210 mm over the three years. Rain falls throughout the year without extreme differences between rainy and dry seasons. Highest precipitation is generally recorded from November to April. Precipitation usually declines in May and remains relatively low until September. Humidity, as well as average temperature and sunlight remain relatively stable across the months throughout the year (Figure 3.2).

I generally categorize the study area as lowland (below 500 meter). However, each sampling block has distinct elevation characteristics. The average elevation, as measured across the camera stations, ranges from 20 m above sea level (m asl.) in Kampar to 219 m asl in Rimbang Baling (Figure 3.3) with the elevation across camera stations for all sites ranging from 6 to 460 m asl. More detailed characteristics of the sampling blocks at the landscape-scale

deemed pertinent to the presence of wildlife, including protection status, total size of the respective forest blocks, and others variables are summarized for each site in Table 3.1.

METHODS

I used existing literature, photographic samples from camera traps, and data from Geographic Information Systems to characterize the ecological aspects of, and investigate the interactions between, wild felids in Central Sumatra. From the literature, I summarized and compared the conservation status, morphological characteristics, and the known life histories of the seven felid species which are thought to occur in Sumatra.

Photographic sampling with camera traps

Photographic samples of wild felids, potential prey, and other carnivores were collected through pilot studies and from systematic camera trap surveys conducted from 2005 to 2007. Pilot camera trapping was aimed at obtaining reliable evidence of the presence of Sumatran tigers and other species of conservation interest across the landscape. The other species of interest mainly constituted the tiger's potential prey and other rare wildlife including smaller felids. The pilot surveys were also used as means of reconnaissance and were conducted throughout the landscape to ensure representation of a variety of environmental conditions. My team and I placed camera traps in areas that we considered to have high likelihood of obtaining tiger pictures. Animal trails, rarely used forest trails, and unused ex-logging road were among the preferred areas for camera placements.

For systematic camera surveys, I drew 45 possible sampling blocks each measuring ~160 km² spaced roughly 10 km apart covering the natural forest areas in the landscape. I selected one sampling block from each of the major forest blocks in which to conduct systematic camera trap

samplings (Figure 3.1). I chose forest types in approximate proportion to their occurrence by sampling two blocks from the peat swamp areas (Kerumutan, Kampar Peninsula), one block from the flat lowland forest in mineral soil (Tesso Nilo), one from the transition between the flat and hilly forests (Peranap), and one from hilly forest (Rimbang Baling). Within each chosen ~160 km² sampling block, I overlaid a 2x2 km grid and selected every other grid cell in which to place the camera station (Figure 3.4). The team identified the best possible camera placement within the predetermined grid cell. In each sampling block the team placed a minimum of 20 camera stations, with additional stations when possible and considered necessary. Although we aimed to deploy all cameras within the pre-determined grid in each sampling block, we occasionally had to adjust the placement to maximize trap success and minimize the risk of vandalism. Cameras were operational 24 hrs per day and remained at the same location for 3 months in systematic surveys, while pilot study surveys ran from one to three months. Every month, we changed film and batteries; cleaned lenses, and replaced broken cameras. Systematic sampling was conducted from May 2005 to November 2007.

In both *ad hoc* and systematic samplings, we used DeerCam[®] film camera traps with film ASA/ISO 200, 36 exposures. We mounted cameras on a tree or a pole at about knee-height. Most stations had a pair of opposing cameras to enable individual identification of tigers and other animals that have individual natural marks used for separate analyses. We placed cameras at ~3 m from the trail on which we expected the animals would pass. In each location where we installed a camera trap, we recorded the GPS coordinates, elevation, the presence of cat and their potential prey based on the observed sign around the location, and the presence of different types of disturbance including logging, encroachment, and hunting.

This study accumulated 7,513 effective trap nights from systematic camera trapping conducted at 104 camera stations in five sampling blocks. Effective trap nights in each sampling block ranged from 1,132 to 1,868 (Table 3.1). For certain analysis, I also used 5,315 effective trap nights of additional sampling accumulated in pilot studies. To model habitat use and interactions between felid species, I considered all samples from both systematic and pilot studies. To compare the photographic rates of felids, prey animals, and other carnivores between sites, I used data only from systematic samplings as each site was sampled with equal effort (although actual effective sampling efforts varied due to different field conditions), allowing more straightforward comparisons.

Species-Trapping Success and Landscape Variables

To investigate factors that influence habitat use by felid species, I considered two different sets of variables. To represent site conditions at the camera station level, I used detection/presence of other species in the camera trap. Based on their detection in camera traps, I calculated the activity level/trap success rate of felids, other carnivores, potential prey animals, and human and used them as predictors variables to model the probability occurrence of each of the five felid species.

For macro-habitat, I used GIS to extract habitat variables within a 500 m radius from each camera station. These variables included distance to major public road, distance to forest centroids, distance to forest edge, distance to centroid of protected areas, precipitation, distance to fresh water, altitude, forest area, percent tree cover, and percent herb cover. Original sources and further details of the extraction and treatment of the data are presented in Appendix 1.

Analyses

To contrast the differences between sites in terms of habitat conditions and the presence of felid species, first I summarized the landscape characteristics, vegetation conditions, and disturbance levels based on literature, GIS data, and field observations. Then, based on the photographic samples I mapped the geographical and altitudinal distributions of felids in the study area.

Finally, I compared the trap success rates for felid species, potential prey, and other carnivores in each sampling block by dividing the number of independent pictures by the level of sampling effort (per 100 trap nights). I considered activity-samples for each species from the same camera station as independent when they were at least 30 minutes apart (Kelly 2003, O'Brien et al. 2003).

Factors affecting the use of habitats

To investigate factors affecting the probability of use of the habitat/site by each felid species, I used single-season occupancy models (MacKenzie et al. 2006) run in Program PRESENCE (Hines 2006). I developed the detection history (the response variable) for each felid species based on the detection non-detection data from camera traps. For site covariates, two different sets of variables were considered. The first set consists of photographic trap rates of every felid species, other carnivores, three different size categories of prey, and humans. Similar to Davis et al. (2010) I categorized potential prey based on their average body mass recorded in the literature, into large (>20 kg), medium size (5 to 20 kg), and small (<5 kg). The second set consists of variables extracted using GIS tools from the available data layers (Appendix 1).

For each set of covariates, I developed models by first entering each covariate in a univariate model. Covariates that improved the model fit compared to the constant model (without covariate) were then combined to develop models with multiple variables. This

approach is similar to that suggested by Thomas et al.(2010). All models were evaluated based on the Akaike Information Criterion (AIC) (Burnham and Anderson 1998).

My general predictions for the first set of covariates were that high level of activity of larger cats, other carnivores, and humans would have negative impacts on the probability of site/habitat use by felids. For the second set of covariates, I predicted that wild felids were less likely to use areas that were more disturbed (closer to road, near the edge), had more rugged terrain (higher altitude), were farther from fresh a water source, and had less vegetation cover.

Assessment of species interaction

I investigated interactions between felid species using two major approaches focused on either spatial- or temporal co-occurrences.

Spatial Co-occurrence

To investigate spatial interactions, I used two-species co-occurrence occupancy models (MacKenzie et al. 2004a, MacKenzie et al. 2006) for every possible combination of felid species that had adequate detection data. There are three possible biological hypotheses that this model has the capacity of testing (MacKenzie et al. 2006): a) do the two species co-occur more or less frequently than expected by chance alone, b) at locations of co-occurrence, are species detections independent from each other, and c) does detection of a species depend on the presence of another species.

I hypothesized that felids with similar body mass, that presumably require similar prey items, would avoid each other. However, I anticipated exceptions for similar sized species that had either distinct morphological characters (e.g., differences in the ratio of canine length to body size) or those that had different physical capabilities (e.g., climbing trees indicating ability to utilize multiple forest strata). The larger the differences in body mass between two species, I

would expect the higher the probability that the felids would co-occur due to higher tolerance or less overlap in resource needs.

Using two-species models, I estimated ϕ , or the Species Interaction Factor (SIF). I considered two species to be avoiding or excluding each other spatially when the value of $\phi < 1$; and they co-occurred more frequently than expected by chance when $\phi > 1$. Two species were considered spatially occurring independently if $\phi = 1$ (MacKenzie et al. 2006). To evaluate the degree of support for these competing hypotheses, I followed the procedures suggested by MacKenzie (2006) by developing two different models and formally comparing their performance based on the differences of AIC values. The first was a full model where each of the three parameters, the probability that the site is used by species A (Ψ^A), the probability that the site is used by species B (Ψ^B), and ϕ was estimated; and the second model where only Ψ^A and Ψ^B were estimated, while ϕ was set to be equal to 1. For each model I evaluated four different scenarios that assume detection probability (P) as either: a) equal and independent (E&I), b) equal and non-independent (E&NE), c) non-equal and independent (NE&I), or d) non-equal and non-independent (NE&NI). The best model from those scenarios was selected (based on AIC and considering any indication of error) and used to estimate Species Interaction Factor (SIF, ϕ) between pairs of felid species.

To assess the spatial co-occurrence, I treated each camera station as the sampling unit or the site. Detection history at each site primarily consisted of three sampling occasions but overall varied from one to five occasions. Each occasion was represented by one-month-long camera trap sampling period involving one or more camera units located within the same 2x2-km grid cell.

Temporal co-occurrence

I focused the investigation of temporal co-occurrence interactions between felid species based on their daily activity patterns. As with the analysis of spatial co-occurrence, independent samples for most species from individual sampling blocks were limited, hence comparing activity patterns between sampling blocks was not considered appropriate due to small sample size. Thus, I pooled data across all sites, including those from systematic sampling and pilot studies. In this approach, I assumed that activity patterns did not vary between blocks. I used a kernel density estimation technique as presented by Ridout and Linkie (2009) to characterize the activity pattern for each species and calculated the coefficient of overlap (Δ) between species. As determined by Ridout and Linkie (2009) via a simulation study, I employed their equation 3.1 kernel estimator with a smoothing parameter (c) of 1.0 to calculate the coefficient of overlap between species.

Mechanisms for coexistence

Based on the findings from the analysis of photographic samples in light of the information from the literature, I identified possible mechanisms used by felids in the study area to maintain coexistence. I ranked the likelihood that each mechanism would be used by each pair of felids. When the differences in characteristics under consideration were extreme, I considered the mechanism promoting co-existence to “most probably” be used by the particular pair of felids. For example differences in prey size preference between large- and small-sized felids are the most extreme. When the difference is only slight, the mechanism is considered as only “likely” used by the pair of species.

RESULTS

Status and characteristics of the wild felids based on literature

Including the unconfirmed records of fishing cats, most sources in the literature noted the presence of seven species of wild felid in Sumatra (Table 3.2). All of the wild felids are protected under Indonesian law (Government Regulation No.7 Year 1999 on the conservation of flora and fauna). Assessing the global status in 2008, IUCN (www.iucnredlist.org) considers all of these felids, except the leopard cat, which is categorized as Least Concern, to be threatened with status ranging from Vulnerable to Critically Endangered.

The seven felid species recorded in Sumatra vary in their morphological characteristics and physical abilities, and in the geographic range of distribution and habitat types in which they live. The cats vary in their average body mass spanning more than an order of magnitude. The smallest is the marbled cat (4 kg) and the largest is the tiger (185.5 kg). Different felids focus on different main prey types ranging from large ungulates for tigers to aquatic animals for flat-headed cats and fishing cats.

Felids in Sumatra also vary in the habitat stratum in which they occur. While most felids dwell in natural forest habitats, some are able to live in relatively disturbed habitats including secondary forests and plantations. Flat-headed cats, fishing cats and leopard cats are all known to be very good swimmers. The first two are particularly recognized as well adapted to wetlands. Clouded leopards and marbled cats have very long tails proportionately to head-and-body length and both are known to have very good to excellent tree-climbing abilities and exhibit semi-arboreal lifestyles (Table 3.2).

According to the literature, four species of felid are either primarily or totally nocturnal and two species can be active at day and night, while one is unknown (Table 3.2).

Wild felids, potential prey and other carnivores: comparison among sites

This study recorded five species of wild felids. Two species, clouded leopards and leopard cats, were photographed in all sampling blocks and were relatively widespread in those blocks (Table 3.3, Figure 3.5 & 3.8). Golden cats were the most restricted in distribution, photographed only in the two blocks that have relatively high elevation: Peranap and Rimbang Baling. Based on their sign, my team and I detected tigers in all sampling blocks, but failed to photograph them in two blocks (Table 3.3). Two species of felid that might be present in the area, flat-headed cats and fishing cats, were not detected in this study.

Rimbang Baling was the only sampling block where all five cat species were photographed. We also detected all five felids, but without photographing tigers, in Peranap. We photographed four felid species in Kerumutan and Tesso Nilo. In Kampar, although we detected three species, we photographed only two of them (Table 3.3, Figure 3.5).

Three felids, tigers, clouded leopards and leopard cats, were present in all sampling blocks (Table 3.3). The golden cat, overall inhabited the highest elevation (mean= 245.8 m) areas in the landscape (Figure 3.6). The clouded leopard and the marbled cat focused their distribution in the medium elevation between 150 to 200 meters above sea level. Meanwhile, two species of extreme sizes - the Sumatran tiger and the leopard cat - both concentrated in the lowest elevations below 100 m.

There was a marked difference in elevations used by the felids in the study area (Figure 3.6). Out of ten possible felid species pairs, there are only two (i.e., between Sumatran tigers and leopard cats, and between clouded leopards and marbled cats) that appear to largely overlap in their altitudinal distribution.

Based on the photographic success rate, the most common large prey were barking deer (*Muntiacus muntjak*) and wild boar (*Sus scrofa*); the most common medium-size prey were pig-tailed macaque (*Macaca nemestrina*) and common porcupine (*Hystrix brachyura*); the most common small prey were mousedeer (*Tragulus spp.*) and Malay civet (*Viverra zibetha*) (Table 3.4).

Considering the potential prey they hold, Peranap was the site that had the highest capture rates of potential prey of all sizes (Figure 3.7). Rimbang Baling, followed by Tesso Nilo, Kampar, and Kerumutan, consecutively, had relatively lower activity level of potential prey.

The presence of other carnivores might also influence the ecological characteristics of felids in the landscape. I identified three mammalian carnivore species/groups deemed likely to compete with felids for prey. These include sun bears (*Helarctos malayanus*), civets (Malay civet *Viverra zibetha* and others from Family Viverridae), and dhole (*Cuon alpinus*). Sun bears were generally common in every area, but the lowest trap rates were found in Peranap (Figure 3.7). Civets reached a peak of trap success rate in the flat dry lowland of Tesso Nilo with rates that were decreasing both toward the lower elevations of peat swamp forests and toward higher elevations of the hill forests. Dholes, which were not recorded in peat land forests, reached their highest trap success rate in Peranap.

Habitat use model

Based on occupancy model developed using site variables calculated from the photographic samples, I found that the probability of site use by leopard cats positively and significantly covaried with the photographic rates of the Sumatran tiger, while site use of the tiger significantly covaried with the photographic rate of non-felid carnivores. Based on the best

model, no other species-trapping success variable significantly covaried with the probability of site use by any felid (Table 3.5a).

Out of ten landscape GIS-extracted variables used in the PRESENCE models, only three were statistically significant factors determining the probability of habitat use by felid species-specific, considering one species at a time. These factors include distance to protected area (covaried negatively with probability of habitat use by tigers and leopard cats), distance to public roads (covaried negatively with probability of habitat use by tigers), and altitude (covaried positively with probability of habitat use by clouded leopards) (Table 3.5b). Based on the best models, no GIS-extracted variables significantly covaried with either golden cats or marbled cats.

Species Interactions

Spatial Co-Occurrence

Based on the point estimates of SIF with value >1 (Figure 3.8), all possible pairs of felid species tended to co-occur more frequently than what can be expected from an independent distribution. This indicates that all felid combination tend to maintain spatial coexistence rather than exclusion. However, only pair between tigers and clouded leopard that show relatively more stable coexistence, as indicated by the strong support for the model ($\Delta AIC=25.3$) and SIF value including standard error that is above 1 (“1” indicates no evidence of spatial aggregation or exclusion). Meanwhile, pair between golden cats and leopard cats somewhat also maintains relatively stable coexistence, as indicated by SIF value including the standard error that is above 1. However, the SIF model for this pair for did received strong support ($\Delta AIC=1.21$).

Out of the ten possible pairs of felid species, models for five of them received strong support based on the difference in AIC and model performance (excluding those that fail to

generate standard error). These include: combinations between Sumatran tigers and three other species (clouded leopards, golden cats, leopard cats, respectively), clouded leopards and golden cats, and clouded leopards and marbled cats. Models for the rest of the felid pairs were either received weak support (based on $\Delta AIC < 0.2$) or performed with some indication of problem (failure to generate standard error).

Models that estimated SIF were considered to have strong support and was concluded to perform better than the constant model when ΔAIC between the two models was > 2 . Models with $\Delta AIC < 2$ were considered to be competitive with respect to support from evidence (Burnham and Anderson 2004).

Except for the pairs between Sumatran tigers and marbled cats and between clouded leopards and marbled cats that show the superiority of models that assume detection between felids as non-independent (NI), models that assume detections between felid pairs as independent (I) performed the best for the rest of the possible pairs of felid species (Figure 3.8).

Temporal co-occurrence

Based on the estimates of activity patterns using KDE on circular data from photographic samples, I found that, except between clouded leopards and marbled cats (estimated coefficient of overlap, $\hat{\Delta}(SE)=0.50(0.08)$), the lowest coefficients of overlap were found between species that were most similar in body size. For example, Sumatran tigers have the lowest overlap with clouded leopard ($\hat{\Delta}(SE)=0.72(0.06)$); golden cats have the lowest overlap with either leopard cats ($\hat{\Delta}(SE)=0.61(0.10)$) or clouded leopard ($\hat{\Delta}(SE)=0.62(0.08)$) (Figure 3.9). Opposite activity patterns were apparent for the following felid combinations: Sumatran tigers and clouded leopards, clouded leopards and golden cats, clouded leopards and marbled cats, golden cats and leopard cats, and leopard cats and marbled cats.

Mechanisms for coexistence

Based on the differences in morphological and ecological characteristics and patterns of spatial and temporal co-occurrence revealed from this study, I identified six possible mechanisms by which felids maintain coexistence. Table 3.6 shows the result of the appraisal based on their relative importance/likelihood.

DISCUSSION

Status and characteristics of the wild felids based on literature

The conservation status determined by IUCN (www.iucnredlist.org) for each species was generally consistent with the vulnerability rank in the action plan developed by Nowell & Jackson (1996) with slight differences due to different criteria used. Based on both assessments, only leopard cats are considered to be safe; all others are threatened with different levels of severity. While IUCN conservation status assessment mainly used the trend in population and distribution (IUCN 2001), Nowell & Jackson (1996) used associations with specific habitat, body size, and geographic range as the criteria to assign vulnerability scores. Nowell and Jackson's criteria can be considered as an inter-specific comparison of the intrinsic characteristics of the species. Meanwhile, IUCN status indicates the level of threats by considering the current ecological aspects of the species. Therefore, I considered both criteria as complementary and useful to prioritize the conservation and management of felids.

Variation in body size and specialization of morphological characteristics are believed to influence preference for different prey animals. Among the most important morphological characteristics of the felids is their body mass relative to canine size, which indicates their ability to kill target prey (Donadio and Buskirk 2006). Based on body mass, most felids < 20 kg are

likely to consume small sized (<5 kg) prey, except the clouded leopard, which based on the relative canine size potentially takes medium-sized prey. Only Sumatran tigers take large animals as their main prey.

Felids also have different proportions of tail to head-and-body length. Longer tails are believed to increase the ability of an animal to stay balanced (Walker et al. 1998). Felids with such characteristics can be expected to have better tree climbing abilities and are possibly also more adapted to steep terrain and therefore can exploit different habitat strata. Climbing skills vary by felid species from occasional climbing to avoid predation/killing, to extremely skillful climbing allowing more intensive use of higher strata for hunting of arboreal prey.

Wild felids, potential prey and other carnivores: comparison among sites

This study detected five out of seven felid species thought to occur in the study area. Based on the trap success rate I ranked the felids from the most to the least common as: leopard cats, tigers, clouded leopards, marbled cats, and golden cats. We did not photograph the flat-headed cats although they were reported to inhabit peat swamps adjacent to Kerumutan/Kampar (Wilting et al. 2010). Factors likely hindering the detection of flat-headed cats in the camera traps were: their extremely low abundance, their possible preference for habitats near freshwater, and their reduced preference for trails. We surveyed peat swamps and riversides, but the sampling effort and techniques in those areas probably were not sufficient/appropriate to detect the cats. We did not find the fishing cat and doubted its existence in the study sites (Sanderson 2009).

Sign of tigers were documented across all sites sampled. However, we failed to photograph tigers in Kampar and Peranap. I suspect that this failure relates to the relatively low abundance of the species likely due to high levels of human disturbance in the two areas as

evidenced by field observation of humans, high trap rates of humans in cameras, and high levels of vandalism of cameras.

The highest diversity of felid species was documented in Rimbang Baling (based only on camera trap pictures) and Peranap (all sign considered). While it was possible that we missed detections of the remaining species in other blocks (Nichols et al. 1998), there appear to be ecological factors that support high felid diversity in Rimbang Baling and Peranap. First, the area had relatively high prey activity (Figure 3.7). Second, the trap rate of tigers was relatively low in Rimbang Baling and zero in Peranap. This would possibly allow other carnivores to use the available food and habitat resources. In addition, Rimbang Baling and Peranap, at least until this study was conducted, were part of relatively large and intact lowland mineral soil forests, in contrast to Tesso Nilo which is relatively small and more isolated. The large and more contiguous habitat would be more likely to accommodate a larger number of species [(Ceballos and Brown 1995), but also see Koh & Ghazoul (2010) and Koh et al. (2010)]. In addition to size, both Peranap and Rimbang Baling cover a transition of altitude and contain more variation in terrain potentially allowing more species niches. Except for golden cats, all other felids were able to inhabit a wide range of elevations. However, I documented marked separation in altitudinal distribution between most pairs of felids in the landscape. The pattern of altitudinal separation that I observed between felids may indicate a possible mechanism for avoiding competition. Between likely-competitors, the felids with the relatively smaller body size tended to be excluded from the seemingly preferred lower altitudes.

I assumed that lowland areas with more gentle terrain would be prime habitat that every species would select in the absence of competition. I also assumed that tigers, having the largest body mass, would be the most dominant species capable of deterring other felids from the prime

altitude. The dominance of larger carnivores over smaller ones has been relatively well documented (Palomares and Delibes 1994, Kamler et al. 2003, Donadio and Buskirk 2006). Smaller felids, especially those with some overlapping prey preference with tigers (such as clouded leopards) would have to shift elevation upward. This could be why I found clouded leopard at higher elevations and golden cats, which overlap clouded leopards, at the highest areas in the landscape.

Felids with extremely small size and little dietary overlap with tigers such as leopard cats and marbled cats do not seem to be competing with tigers hence they can also inhabit the prime elevation. Between the two, however, they have nearly opposite daily activity patterns; thereby maintaining spatial coexistence.

Unlike felids, other carnivores, particularly Malayan sun bears and civets, did not seem to avoid tigers. The trap success rate of this group of animals was relatively high and seemingly independent from the activity level of tigers. Although body mass was relatively close compared to other felids, tigers and sun bears consume distinctly different food items (Servheen et al. 1999). Meanwhile, sun bears are also capable of climbing trees and utilizing other forest strata allowing them to further avoid competition with tigers. As for dholes, however, there is high overlap with tigers in diet. Therefore, as I would expect, except in peatland, the trap success rate of dholes was depressed in areas with tigers, suggesting avoidance (Figure 3.7).

Habitat use model

Using species-trapping success covariates the models showed two variables impacted probability of use by different felid species. The probability of site use by leopard cats covaried positively with the trap success rate of the tiger; while probability of habitat use by the tiger covaried positively with the trap success rate of non-felid carnivores. Instead of indicating causal

relationship, I believe these results signify the tolerance between these animal taxa. It was surprising that other factors such as human use or other large felid use did not impact felid use/occurrence. This may be due to limitations of sample size, particularly the low detection rates for certain felids, or due to data pooling across sites.

As expected, the probability of habitat use by tigers and leopard cats covaried negatively with distance to protected area centroids such that when moving away from the centroid of protected areas, it became less likely for the site to be used by either species. However, it was surprising that this factor significantly impacted only these two species and not three others. Equally surprising was the fact that leopard cats were impacted by the distance to centroids of protected areas since it seemed that they could occur almost anywhere. Leopard cats could just be responding to the tiger's "umbrella" and lack of the other mid-sized competitors. Similarly, it is also difficult to explain why other landscape variables that I would expect to have significant impacts did not do so. For example, I expected distance to centroid of large forest block and proportion of forest area to have similar impact as distance to centroid of protected area.

The fact that water-related variables, namely 'distance to water' and 'precipitation', did not significantly impact probability of use by felids was understandable since the study area had ample water throughout the year (Figure 3.2). In addition, every point in the landscape was relatively close to either a river network or water body.

The impact of roads on tigers was somewhat contrary to my expectation especially in light of findings from other studies in Kerinci (Linkie et al. 2006). Unlike in Kerinci-Seblat National Park, which has a relatively intact large forest block, forests in the study area are much more fragmented with public roads separating one forest block from the others. Furthermore, the

flat lowland forest of Tesso Nilo, which supports the highest density of tigers (Sunarto et al. 2010b), is relatively small in size and is surrounded by major public roads.

Species Interaction Factors

Spatial Co-Occurrence

All felid species generally tended to maintain spatial coexistence albeit with small possibility to exclude each other.

Although both descriptive statistics and habitat models indicated that clouded leopard tended to avoid tigers by disproportionately utilizing higher elevation, clouded leopards apparently still had large degree of spatial overlap in their occurrence with tigers. Based on the estimate of SIF and the standard error for these two species that did not include 1, suggests the two species tended to co-occur more frequently than expected (which might be expected due to their large overlap in prey items), but they also tend to maintain co-existence (which appear to be possible due to the arboreal nature of clouded leopard, allowing this species to utilize higher forest strata).

Although smaller in body size than tigers, clouded leopards have the largest canines relative to the body size of all felids (Nowell and Jackson 1996), allowing them to kill prey animals that are proportionately larger than expected based on the predator's body mass. With the absence of very large prey (such as gaur or wild buffalo) in the study area, competition between tigers and medium size felids may be expected. Unlike other areas with large prey, Sumatra lacks these prey types, except for the feral buffalo in a very small area in the southwestern tip of the island. The lack of large prey is believed to have forced tigers in Sumatra to prey upon relatively smaller ungulates. This likely has consequences for clouded leopards and golden cats, and possibly could explain the absence of common leopards (*Panthera pardus*) from

Sumatra (Kitchener, 1999). Compared to other places, clouded leopards in Sumatra live in much lower density (Hearn et al., 2008; Hutajulu et al., 2007), potentially due to competition with tigers. The fact that clouded leopards generally occur at higher density when densities of larger cats are lower has also been reported from several places in the mainland Asia (Grassman Jr. et al., 2005; Sanderson et al., 2009). Furthermore, with the absence of tigers, clouded leopards are even suspected to be less nocturnal in Borneo (Nowell and Jackson, 1996).

Temporal co-occurrence

Activity patterns of tigers and leopard cats, in this study, were generally consistent with those documented in the literature (Table 3.2). However, this was not the case with three other felid species. Clouded leopards are generally known to be active at day and night but were found to be primarily nocturnal in this study. Golden cats are generally also known to be active at day and night, but instead were found to be primarily active during the day resembling the pattern documented in Kerinci Seblat (Ridout and Linkie 2009). Marbled cats are known to be active primarily at night (Nowell and Jackson 1996, Grassman Jr et al. 2005). However, this study found this species was primarily active during the day, opposite from what is documented in the literature.

I found that only tigers' and leopard cats' daily activity patterns were consistent with the literature: tigers were active both day and night, while leopard cats were primarily active at night. Assuming that daytime is the prime time that felids would select in the absence of competition, this could suggest the dominance of tigers, pushing species with smaller body size to adjust their activity to avoid competition. Compared to other felids, tigers have the lowest level of temporal activity overlap ($\hat{\Delta}$) with clouded leopards, the felid most likely competing due to overlap in prey.

This study found that species with similar size or similar prey size generally had low coefficients of temporal activity overlap, suggesting temporal avoidance. Similarly, species inhabiting a similar guild such as clouded leopards and marbled cats (both of which are good tree climbers) showed relatively low overlap. Specialization in temporal scale could indicate the scarcity of food items available for the competing species (Schoener 1974a). Interestingly, this study found that temporal avoidance was generally apparent between species with most similar traits, particularly body mass.

Mechanisms for coexistence

Through experiments, Gause (1934) showed that organisms with similar needs will not be able to coexist in the long-term. However, every organism has unique multi-dimensional characteristics allowing them to partition resources and thereby maintain coexistence with other species that have similar resource needs (Schoener 1974b).

As suggested by Schoener (1974b), I found that different felid species were able to maintain coexistence with other sympatric felids through resource partitioning in various ways. Pairs of species exhibited different mechanisms to maintain coexistence. For example, at the landscape-scale, golden cats appeared to use geographical separation to maintain coexistence with other felids. Meanwhile, separation in elevation most probably facilitated coexistence between golden cats and leopard cats, and between marbled cats and leopard cats (Table 3.6, Figure 3.6).

Separation in vertical strata is most probably used by pairs of species that have high diet overlap but differ in their ability to climb trees such as between tigers and clouded leopards. Temporal avoidance is most probably operating in three pairs of felids namely clouded leopards and golden cats, clouded leopards and marbled cats, and marbled cats and leopard cats.

Assuming there is no issue related to prey activity patterns, focusing their activity on certain times of day when others were less active would allow a felid species to exploit similar resources with minimum interference from other species. Time separation is probably the next choice when spatial and prey separations are not adequate. Food size does matter and, particularly for carnivores, they generally have strict lower and upper prey size limits (Elton 1927).

Management implications

To maintain and promote felid diversity, we need to understand not only how to provide habitat required by each of the felid species, but also how to anticipate inter-specific interactions that might prevent certain species from inhabiting certain habitat. Results of this study suggest that felid diversity can be promoted in different ways. At the broader scale, representation of different forest types is one prerequisite to accommodate felids that inhabit unique habitat types. At the finer scale, an area that contains a mosaic of habitats with a variety of vegetation and landscape features, is more likely to accommodate more species than one dominated by just a few or a single habitat type. Providing greater variety of habitat types, however, has a consequence of limited area available for each type. Without habitat modification and intensive management, it is unlikely that both high species diversity and population abundance can be achieved at the same time in the same area. The common rule that the biomass availability dictates the number of carnivores that can live in a given area has been demonstrated by Carbone and Gittleman (2002). Habitat modifications along with enrichment of prey species preferred by certain felids are ways to achieve higher population abundance. While small felids will survive with small size prey, large cats (with body mass at least 21.5 kg), due to their energetic constraints, require larger sized prey, preferably much larger than their own size (Carbone and Gittleman 2002)

If managers choose to promote only species with large body mass, this might result in a decline in smaller species if ‘mesopredator release’ and ‘trophic cascade’ phenomena operate in that system. It has been documented in some areas that ‘mesopredator release’ might happen when the top predator is removed from an area, releasing smaller predators or prey from competition (Crooks and Soule 1999, Henke and Bryant 1999, Gehrt and Prange 2007). Mesopredator release, or sudden explosion of smaller predator populations might cause smaller prey to be depleted, further triggering sudden changes in lower trophic levels, a phenomenon commonly known as “trophic cascade” (Mills 2007). This implies that there is a need to evaluate, at the landscape level, the effectiveness of the use of certain species (particularly with largest body size) as an umbrella species. However, a recent study investigated the coexistence of four sympatric carnivore species in Belize (Davis et al. 2010) found no evidence that the presence of jaguar interferes with smaller carnivores. Davis et al. (2010) believe that providing good habitats for the jaguar also indirectly aids other carnivore species.

Rimbang Baling, and other lower slopes of the hilly areas, harboring all the species found in this study, are likely to be suitable as high diversity areas. However, not all cat species can be accommodated in each place. For example, wetland-dependent species with distributions mostly limited to the coastal areas such as the flat-headed cat, might not find a good habitat in higher lands. In terms of population abundance, peat areas are unlikely to support high abundance for most species. In this setting, it might be expected that competition (particularly inter-specific) is more intense. Most large- and medium-sized cats likely live in low densities bringing up issues of inbreeding and viability for endangered species.

Results from Tesso Nilo suggest that both tigers and leopard cats can live at their highest density in flat lowland forests in mineral soil, likely coexisting due to their extreme difference in

body size and prey preference. With these two species living in relatively high abundance, it is hypothesized that there probably is very little space left for other felids. The relatively low capture rates for two medium-sized felids, clouded leopards and golden cats, in flat lowland forest of Tesso Nilo indicate their relatively lower adaptability in such habitat types; while tigers and leopard cats potentially out-compete them in this habitat. Clouded leopards' ability to use different habitat strata perhaps evolved in response to such competition.

The Tesso Nilo forest block, being a logged-over area, relatively isolated, and having a mix of secondary forests, might not represent the conditions of fully pristine forests. In many places of Sumatra, however, lowland forests have either already completely disappeared or remained as degraded logged-over and isolated forests. Massive deforestation in Sumatra (Forest Watch Indonesia and Global Forest Watch 2001, Holmes 2002, Kinnaird et al. 2003a, Uryu et al. 2007) mostly took place in flat dry lowland areas; yet the remaining forests – even degraded ones – are still valuable from a conservation point of view. Others have demonstrated the high value of degraded forest for the conservation of tigers and other animals (Linkie et al. 2008a, Rayan and Mohamad 2009). This study and other analysis (Sunarto et al. 2007) showed that Sumatran tigers can achieve their highest abundance in flat lowland forests. Protection of the remaining flat lowland forests is required to maintain the increasingly threatened, forest-dependent felids.

Results from this study suggest that peat swamp forests are less likely to support high diversity or density of felids due to the naturally low productivity coupled with occasional flooding that prevents strictly terrestrial animals from using them. However, this does not necessarily lower conservation value of such areas. Certain felid species are highly dependent on wetland habitats and are unlikely to thrive in drier lands. In addition to benefiting water-dependent felids and other rare wildlife, protection of peat swamp habitats is important from the

hydrological perspective (Moore 1987), and to ensure that global climate change due to excessive release of CO₂ will not worsen (Uryu et al. 2007).

Conclusion

This study has demonstrated that inter-specific interaction is a factor likely to influence the success or failure of felid community management. In addition to gaining knowledge pertinent to the species of management interest, understanding the interactions between species within the community is important for effective conservation and management. This study also demonstrated, however, that most felid species have the ability to maintain coexistence. The mechanisms include the use of different conditions of habitats, use of different prey sizes, use of different geographical areas, finer scale spatial separation, and temporal separation in activity patterns.

Further investigations are needed to provide answers to several questions that remain. For example, to manage the felid community effectively, we need to know the prey items available and those actually consumed by each felid species in Sumatra. Understanding diet for each species is particularly crucial to indicate the intensity of competition between species. Furthermore, since natural habitats in the region have become increasingly fragmented, it is important to understand the level of connectivity, or isolation, between sub-populations of felids in the landscape. Availability of such information will facilitate management efforts designed to promote conservation of the felid guild across the landscape.

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Table 3.1. Characteristics of five sampling blocks in Central Sumatra and levels of systematic sampling effort conducted from 2005 to 2007.

	Kampar	Kerumutan	T.Nilo	Peranap	R.Baling
Major soil type	Peat	Peat	Mineral	Mineral	Mineral
Composite criteria*	Alluvial and swamp	Alluvial and swamp	Sedimentary	Sedimentary	Metamorphic
Protection status	No-protection	Wildlife Reserve	National Park	No-protection	Wildlife Reserve
Ex-logging concession	Yes	No	Yes	Yes	Partly
Observed logging impact	High	Low	Very High	Medium	Low
Terrain	Flat	Flat	Generally flat	Flat to gentle hill	Gentle to steep hill
Wetness	Mostly inundated	Mostly inundated	Mostly Dry	Dry	Dry
Total size of core forest block (in 1,000 ha) **	306	379	86	186	168
Sampling period	20Jul07-03Nov07	7Sep06-17Dec06	31May05-11Sep05	16Sep05-29Dec05	19Apr06-28Jul06
# Trap Stations***	18	22	22	22	20
Effective Trap Nights	1,132	1,868	1,618	1,321	1,574
Camera loss	16	0	3	3	0
Human pictures	28	1	85	17****	11

*Combination of geological, bioclimatic, geomorphological and topographical maps as identified

by Laumonier (1997); ** Obtained by measuring the forest area based on interpretation of

Landsat images acquired in 2007 (done by WWF Indonesia GIS Team) after reducing with 3 km

buffer, assuming edge effect; *** Counted based on the position in 2x2 km grids. For the case of

cameras being moved during sampling period due to security or other reasons, they are

considered as one trap station if location is still in the same 2x2 grid. Total loss/failure of

cameras in a given grid during sampling period render the trap station being uncounted; ****

Includes the presence of forest dweller indigenous people who live on subsistence hunting, but

not researcher presence

Table 3.2. Characteristics of the felid species based on literature*.

	Sumatran tiger	Clouded leopard	Golden cat	Marbled cat	Leopard cat	Flat-headed cat	Fishing cat
IUCN 2008 Status	Critically Endangered	Vulnerable	Near Threatened	Vulnerable	Least Concern	Endangered	Endangered
Vulnerability rank¹	Highest	Very High	High	High	Very Low	High	High
Average body weight² (kg)	185.5	20.5	11	4	4.75	4.75	10.25
Proportion of tail to head and body³	0.4-0.6	0.7-0.9	0.5-0.6	1-1.1	0.4-0.6	0.2-0.3	>0.5
Main prey	Ungulates >20 kg ⁴	Primates, medium-sized mammals ⁵	Small- to medium-sized vertebrates ^{1,6}	Small vertebrates ¹	Small vertebrates ⁷	Aquatic animals ^{1,8}	Aquatic animals ⁸
Main Habitat	Natural & semi disturbed Forests,	Closed forest ⁵	forest ^{1,5}	Moist forest ¹	Forest, plantation, suburban ³	Riparian ⁹	Tidal forests ⁸
Stratum	Strictly terrestrial	Semi-arboreal ⁵	Terrestrial	Semi- arboreal ⁵	Mostly terrestrial	Semi- aquatic ⁹	Semi- aquatic
Ability to climb	Bad	Excellent ¹	Good ⁶	Very good ¹	Very good ⁷	Unknown	Unknown

Table 3.2. Characteristics of the felid species based on literature*.

	Sumatran tiger	Clouded leopard	Golden cat	Marbled cat	Leopard cat	Flat-headed cat	Fishing cat
Ability to swim	Good	Unknown	Unknown	Unknown	Very good ⁷	Very good ⁸	Very good ⁸
Activity pattern	Day & night ^{11,12}	Day & night ^{1,11,12}	Day & night ^{1,11,12}	Primarily nocturnal ^{5,1}	Primarily nocturnal ⁷	Unknown	Nocturnal ¹⁰

*) Main sources: 1) Nowell & Jackson (1996), 2) Inskip and Zimmermann (2009), 3) Corbet and Hill (1992), 4) Karanth and Smith (1999), 5) Grassman et al. (2005), 6) Kawanishi and Sunquist (2008), 7) Santiapillai and Suprahman (1985), 8) Melisch et al. (1996), 9). Bezuijen (2000), 10) Sanderson et al. (2008), 11) Ridout and Linkie (2009), 12) van Schaik and Griffiths (1996).

Table 3.3. Distribution and detection of felid species in five sampling blocks

	Kampar	Kerumutan	T.Nilo	Peranap	R. Baling
Sumatran Tiger	Present (sign & previous camera trapping), not detected in current camera trap sample	Detected in camera trap	Detected in camera trap	Present (sign and information), not detected in camera trap	Detected in camera trap
Clouded leopard	Detected in camera trap	Detected in camera trap	Detected in camera trap	Detected in camera trap	Detected in camera trap
Golden cat	Likely absent	Likely absent	Unknown	Detected in camera trap	Detected in camera trap
Marbled cat	Likely present, not detected	Detected in camera trap	Detected in camera trap	Detected in camera trap	Detected in camera trap
Leopard cat	Detected in camera trap	Detected in camera trap	Detected in camera trap	Detected in camera trap	Detected in camera trap
Flat-headed cat	Likely present, not detected	Present, not detected in camera trap	Unknown	Likely absent	Likely absent

Table 3.4. Potential prey available in the study area as identified from camera trap pictures

Scientific Name	Group Size	Indep. Picture	Activity Index*)	Average Weight (kg)	Prey Category
<u>Aves</u>					
<i>Chalcopaps indica</i>	1	7	0.09	0.124 ^{a)}	Small
<i>Rollulus rouloul</i>	2.7	7	0.09	0.217 ^{a)}	Small
<i>Gallus gallus</i>	1.09	10	0.13	0.672 ^{a)}	Small
<i>Lophura erythrophthalma</i>	1.23	41	0.55	0.94 ^{a)}	Small
<i>Lophura ignita</i>	1	8	0.11	1.9 ^{a)}	Small
<i>Argusianus argus</i>	1	60	0.80	1.95 ^{a)}	Small
<i>Ciconia stormi</i>	1	4	0.05	2.185 ^{a)}	Small
<u>Mammalia</u>					
<i>Tupaia sp.</i>		5	0.07		
/TUPAIIDAE	1			0.05 ^{c*)}	Small
<i>Rattus sp.</i> */MUROIDEA	1	25	0.34	0.151 ^{*)}	Small
<i>Callosciurus sp.</i> */SCIURIDAE	1	7	0.09	0.825 ^{c*)}	Small
<i>Herpestes brachyurus</i>	1.1	11	0.15	1.4 ^{b)}	Small
<i>Trichys fasciculata</i>	1	6	0.08	1.75 ^{c)}	Small
<i>Hemigalus derbyanus</i>	1	13	0.17	2.1 ^{b)}	Small
<i>Martes flavigula</i>	1	6	0.08	2.15 ^{c)}	Small
<i>Aonyx cinerea</i>	2.42	6	0.08	3 ^{f)}	Small
<i>Paradoxurus hermaphroditus</i>	1	13	0.17	3.4 ^{b)}	Small
<i>Viverra zangalunga</i>	1	81	1.09	3.7 ^{b)}	Small
<i>Tragulus spp.</i>	1.03	150	2.01	3.85 ^{b)}	Small
<i>Macaca fascicularis</i>	2.02	10	0.13	4.5 ^{b)}	Small
<i>Cynogale benettii</i>	1.14	5	0.07	4.7 ^{b)}	Small
<i>Paguma larvata</i>	1	5	0.07	4.8 ^{b)}	Small
<i>Macaca nemestrina</i>	1.48	607	8.14	6.5 ^{b)}	Medium
<i>Presbytis melalophos</i>	1	8	0.11	6.6 ^{b)}	Medium
<i>Presbytis femoralis</i>	1	1	0.01	7 ^{b)}	Medium
<i>Arctictis binturong</i>	1	6	0.08	7.5 ^{c)}	[Medium]
<i>Hystrix brachyura</i>	1.12	187	2.51	8 ^{d)}	Medium
<i>Arctonyx collaris</i>	1	6	0.08	10.5 ^{b*)}	Medium
<i>Cuon alpinus</i>	1.16	12	0.16	17 ^{b)}	[Medium]
<i>Muntiacus muntjak</i>	1.01	235	3.15	21 ^{d)}	Large
<i>Helarctos malayanus</i>	1.02	139	1.86	56 ^{d)}	[Large]
<i>Sus barbatus</i>	1.08	27	0.36	85 ^{c)}	Large

Scientific Name	Group Size	Indep. Picture	Activity Index*)	Average Weight (kg)	Prey Category
<i>Sus scrofa</i>	1.33	112	1.50	125 ^{b)}	Large
<i>Cervus unicolor</i>	1.02	26	0.35	249.5 ^{b)}	Large
<i>Tapirus indicus</i>	1.03	127	1.70	225 ^{b)}	(Large)
<i>Elephas maximus</i>	1.04	12	0.16	4000 ^{c)}	(Large)
<u>Reptilia</u>					
<i>Varanus salvator</i>	1	1	0.01	37.5	<Large>

*) Also called trap success rate or known as Relative abundance Index (O'Brien et al. 2003), calculated as independent pictures/100 trap nights

Note: Potential prey are classified based on the average weight into small (<5 kg), medium (5 to 20 kg), and large (>20 kg) and presented, for each class, in the order of average weight.

^{a)}(Dunning 2007), ^{b)}(MacDonald 2006), ^{c)}(Francis 2008), ^{d)}(Kawanishi and Sunquist 2004),

^{e)}(Ruiz-Olmo et al. 2001)

Based on closely related species of similar size ^{f)}(Busch Entertainment Corporation 2009)

[] carnivore, potential cat's competitor

() few evidence of being prey

<> cold-blooded, unlikely to be detected with camera trap's

Table 3.5a. Output of occupancy models (MacKenzie et al. 2006), showing the relationships among species-trapping success variables and the use of sites by five felid species. Numbers show untransformed estimates of coefficients for covariates (betas) and standard error in parentheses; values of covariates were all normalized before being entered in the model. Bold values indicate significant differences from 0. Note: NA indicates not applicable.

Parameter	Sumatran tiger		C. leopard		Golden cat		Leopard cat		Marbled cat	
	Best model	Model average	Best model	Model average	Best model	Model average	Best model	Model average	Best model	Model average
Intercept	-1.38 (0.22)	-1.38	0.97 (0.37)	-0.94	-2.28 (1.10)	-2.38	0.03 (0.41)	-0.02	-1.25 (0.91)	-0.95
Sumatran tigers	NA	NA		0.00		-0.01	2.27 (1.04)	2.28	NA	0.00
Clouded leopard	NA	NA		NA	1.68 (1.55)	0.85	NA	NA	NA	0.00
Golden cat	NA	NA	0.42 (0.38)	0.27		NA	NA	NA	NA	NA
Leopard cat	NA	NA		NA		NA	NA	NA	NA	0.00
Marbled cat	NA	NA		NA		NA	NA	NA	NA	NA
Malayan sun bear	NA	NA		0.00		0.00	NA	NA	NA	0.67
Dhole	NA	NA	0.70 (0.64)	0.56		0.00	NA	NA	NA	NA
Non-felid carnivores	0.65 (0.19)	0.62		0.00		0.00	0.44 (0.24)	0.32	NA	0.55
Large prey	NA	0.00		0.04		0.10	NA	NA	NA	0.01
Medium prey	NA	0.00		0.00	0.68 (0.36)	0.49	NA	NA	1.99 (1.24)	1.05
Small prey	NA	0.00		0.00		0.00	NA	0.03	NA	0.00
Humans	NA	0.12		0.00		0.00	NA	NA	NA	0.00

Table 3.5b. Output of occupancy models (MacKenzie et al. 2006), showing the relationship among GIS-extracted landscape variables and the use of habitat by five felid species. Numbers show untransformed estimates of coefficients for covariates (betas) and standard error in parentheses; values of covariates were all normalized before being entered in the model. Bold values indicate significant difference from 0. Note: NA indicates not applicable.

Parameter	Sumatran tiger		C. leopard		Golden cat		Leopard cat		Marbled cat		
	Best model	Model average	Best model	Model average	Best model	Model average	Best model	Model average	Best model	Model average	
Intercept	-3.56 (0.71)	-3.36	-0.51 (0.35)	-0.49	-11.72 (16.83)	-6.09	-1.11 (0.57)	-1.13	1.19	(1.75)	0.39
Distance to forest edge (m)	NA	-0.11	NA	-0.27	NA	0.02	NA	0.00	NA	0.02	0.02
Distance to centroid of protected area (m)	-1.57 (0.45)	-1.53	NA	NA	NA	-0.02	-1.35 (0.43)	-1.34	NA	NA	0.00
Distance to centroid of large forest block (m)	NA	NA	NA	NA	NA	-0.03	NA	0.00	NA	NA	-0.01
Distance to major public road (m)	-2.96 (1.11)	-2.74	NA	NA	NA	-0.03	NA	0.01	NA	NA	0.00
Distance to water (m)	NA	0.07	NA	NA	NA	NA	NA	-0.05	NA	NA	0.00
Precipitation (mm)	NA	NA	NA	-0.46	NA	NA	NA	0.00		-5.69 (4.36)	-2.40
Altitude (m)	NA	NA	2.97 (1.01)	3.51	NA	NA	NA	0.00		11.78 (7.02)	6.42
Forest area (ha)	NA	NA	NA	NA	16.57 (27.11)	0.06	NA	0.00		NA	0.08
Tree cover (%)	NA	-0.15	NA	NA	NA	7.01	NA	-0.01		NA	0.00
Herbaceous plant cover (%)	NA	0.05		NA			0.90 (0.47)	0.85			-0.01

Table 3.6. Possible mechanisms to maintain coexistence between felid species

Pair of felid species		Possible Mechanism					
		Geographic	Elevation	Vertical strata	Micro-habitat*	Active time	Prey size
Sumatran tiger	Clouded leopard	-	√√	√√√	√	√√	√
Sumatran tiger	Golden cat	√√	√√	√	√	-	√√
Sumatran tiger	Marbled cat	-	√	√√	√	√	√√√
Sumatran tiger	Leopard cat	-	-	√	√√	√	√√√
Clouded leopard	Golden cat	√√	√	√	√	√√√	√
Clouded leopard	Marbled cat	-	-	-	-	√√√	√√
Clouded leopard	Leopard cat	-	√√	√	√√	√√	√√
Golden cat	Marbled cat	√√	√	√	√	-	√√
Golden cat	Leopard cat	√√	√√√	√	√√	√√	√√
Marbled cat	Leopard cat	-	√√√	√	√√√	√√√	-

Notes: √√√=most probably, √√=very likely, √ = likely; - = unlikely; * including presence of other species

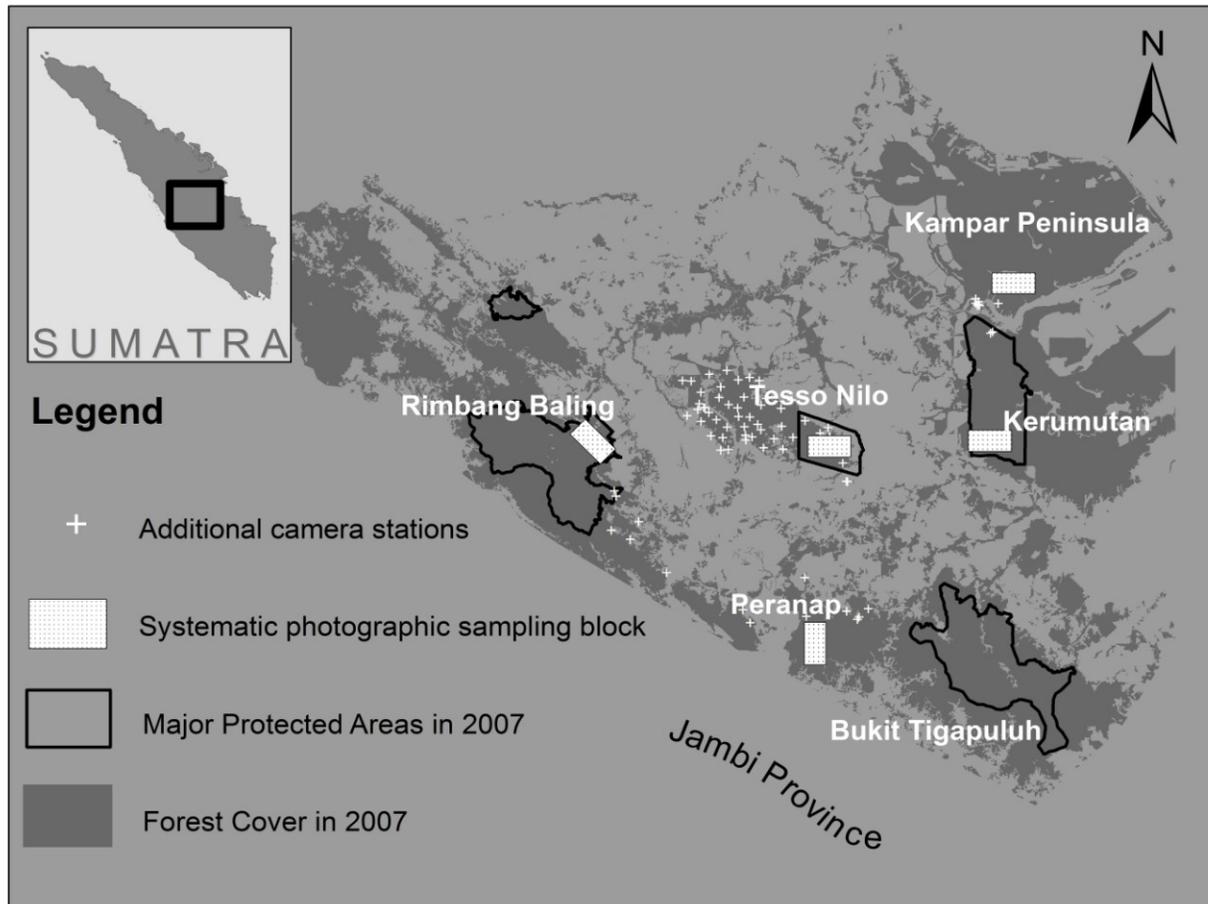


Figure 3.1. Map of study area showing existing forests, major protected areas, and position of camera trap sampling blocks and stations in Riau Province, central Sumatra.

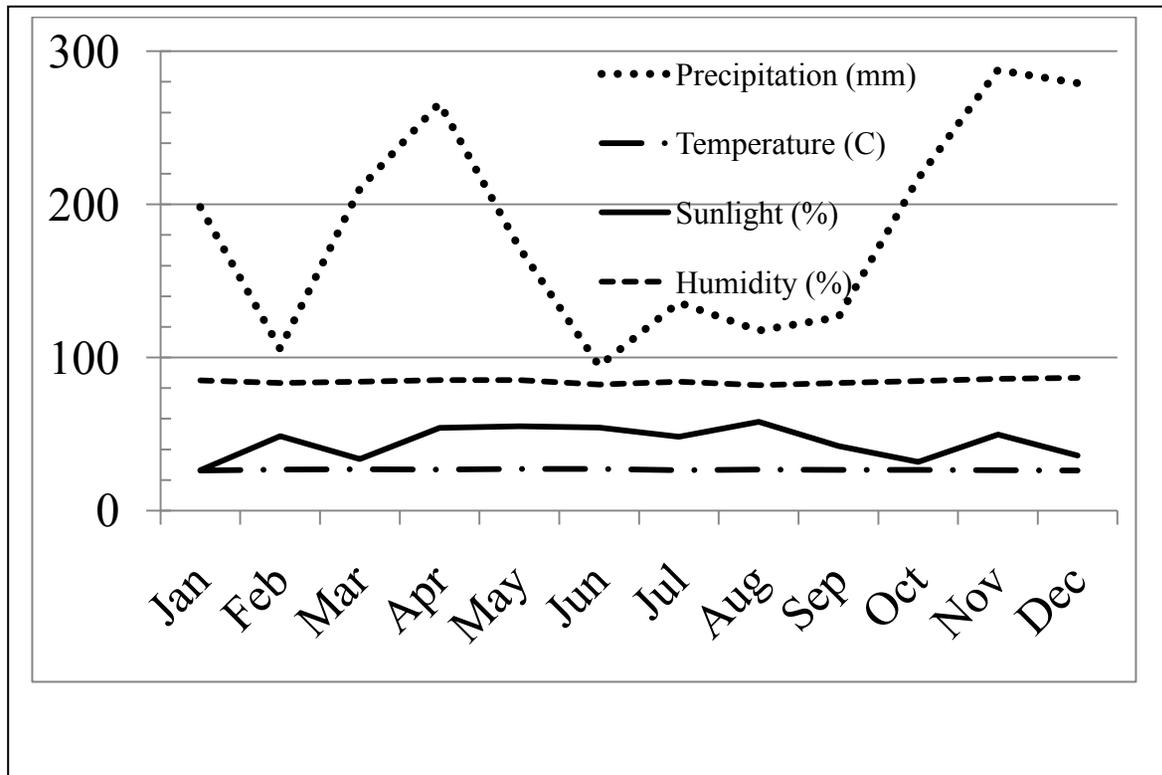


Figure 3.2. Climate data from the study area, averaged from 2004 to 2006. Data collected at weather station in Rengat (102.32 E, 0.47 S), provided by Badan Meteorology dan Geofisika Wilayah I Riau).

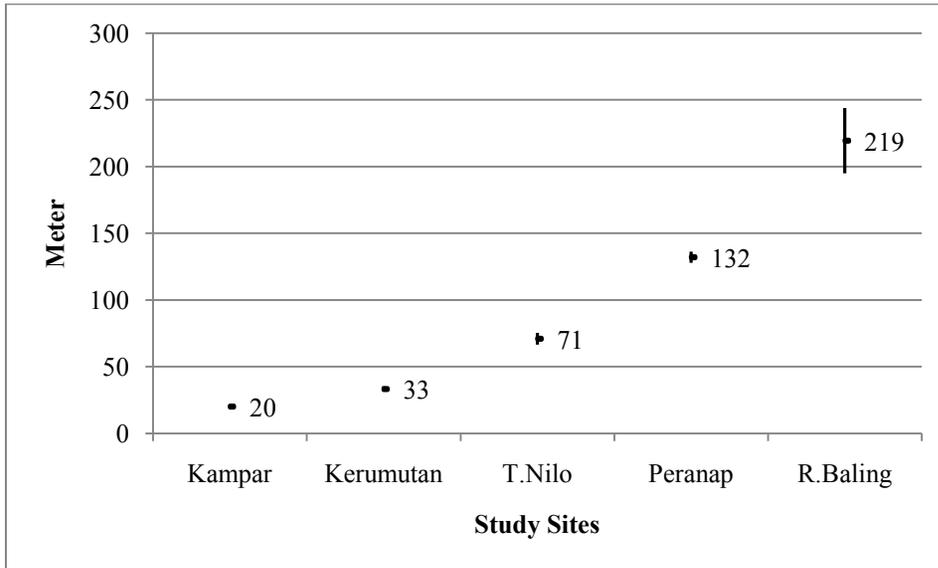


Figure 3.3. Average elevation and standard error of the sampling blocks as measured in every trapping site.

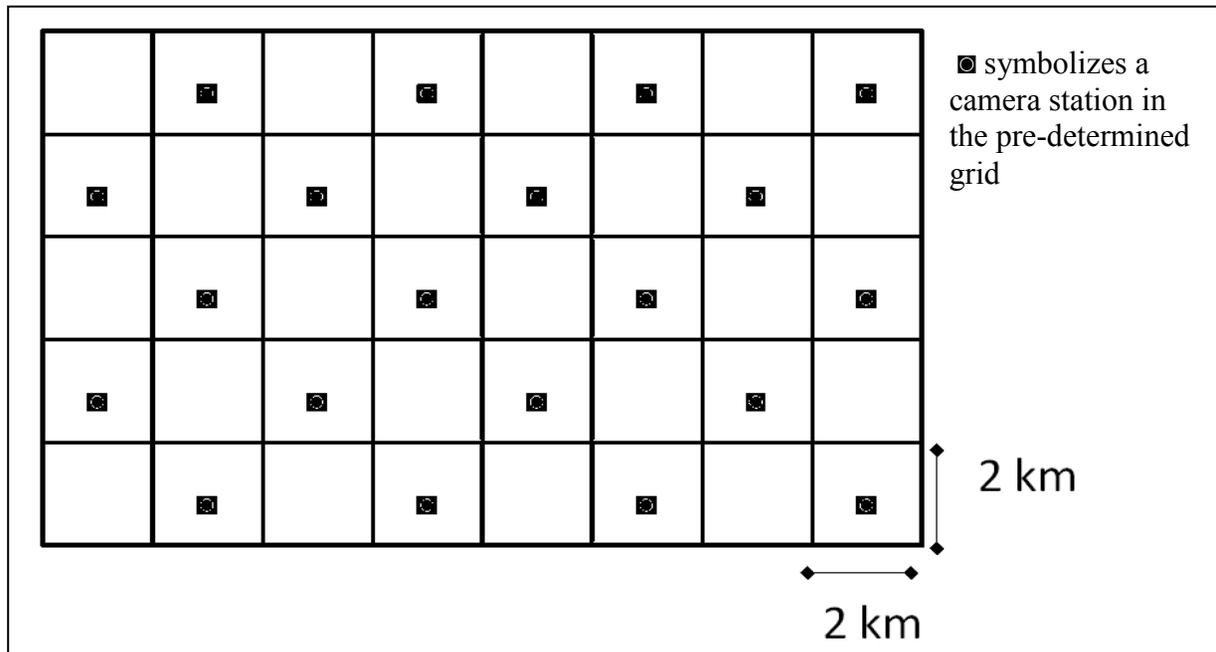


Figure 3.4. Camera placement study design within a sampling block showing that cameras were to be placed in every other grid cell.

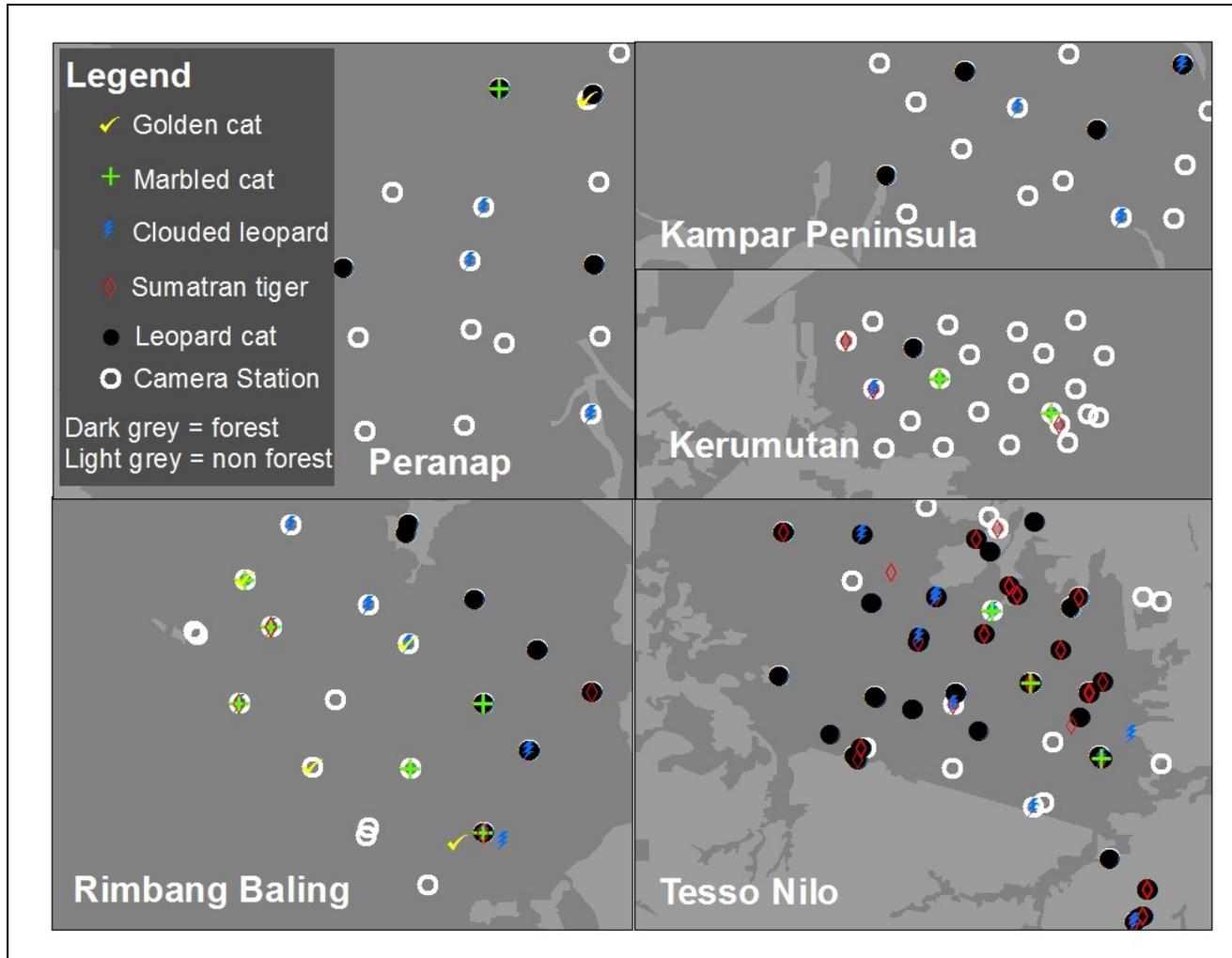


Figure 3.5. Map showing felid presence based on photographic data from five sampling blocks in Central Sumatra.

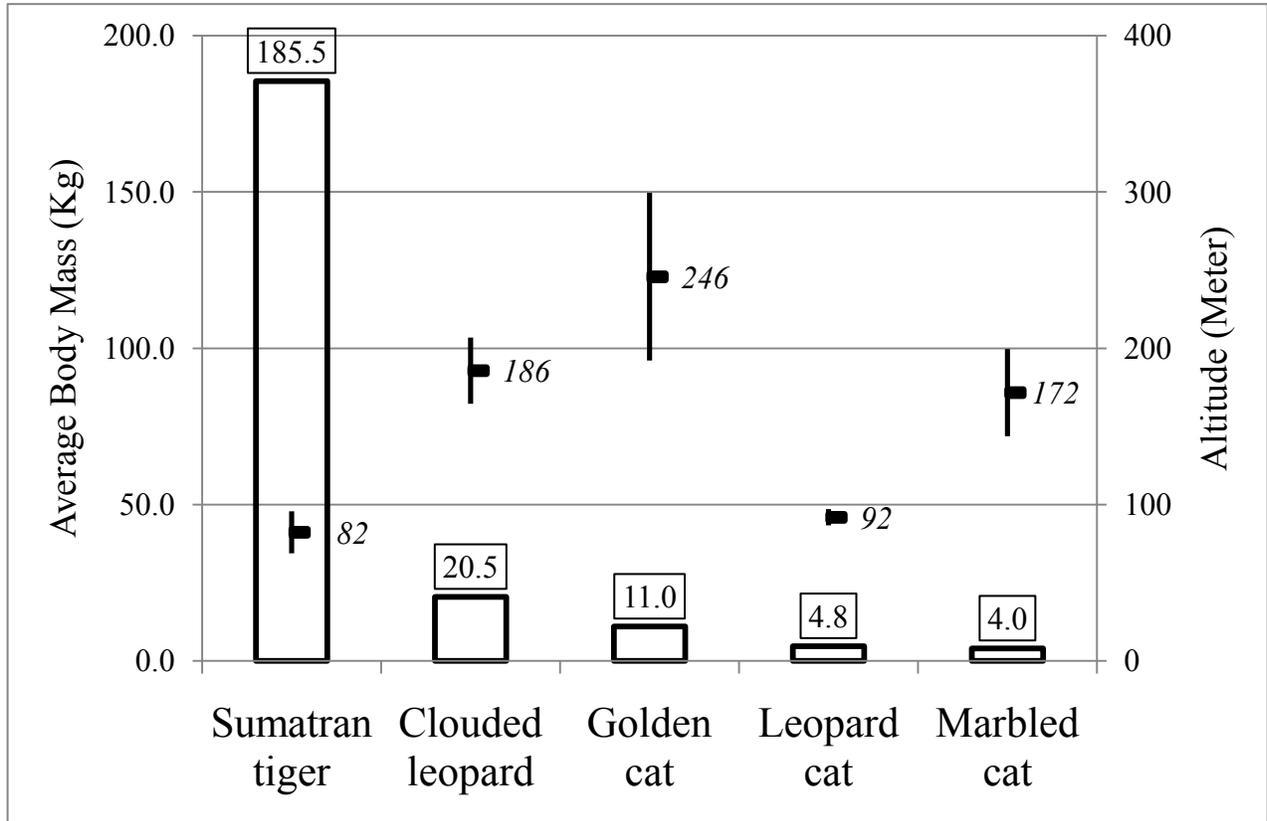


Figure 3.6. Known average body mass (bars) and altitudinal distribution of felid photo-captures in the landscape. Altitudinal values indicate mean+SE of elevation of all camera traps where respective species was captured.

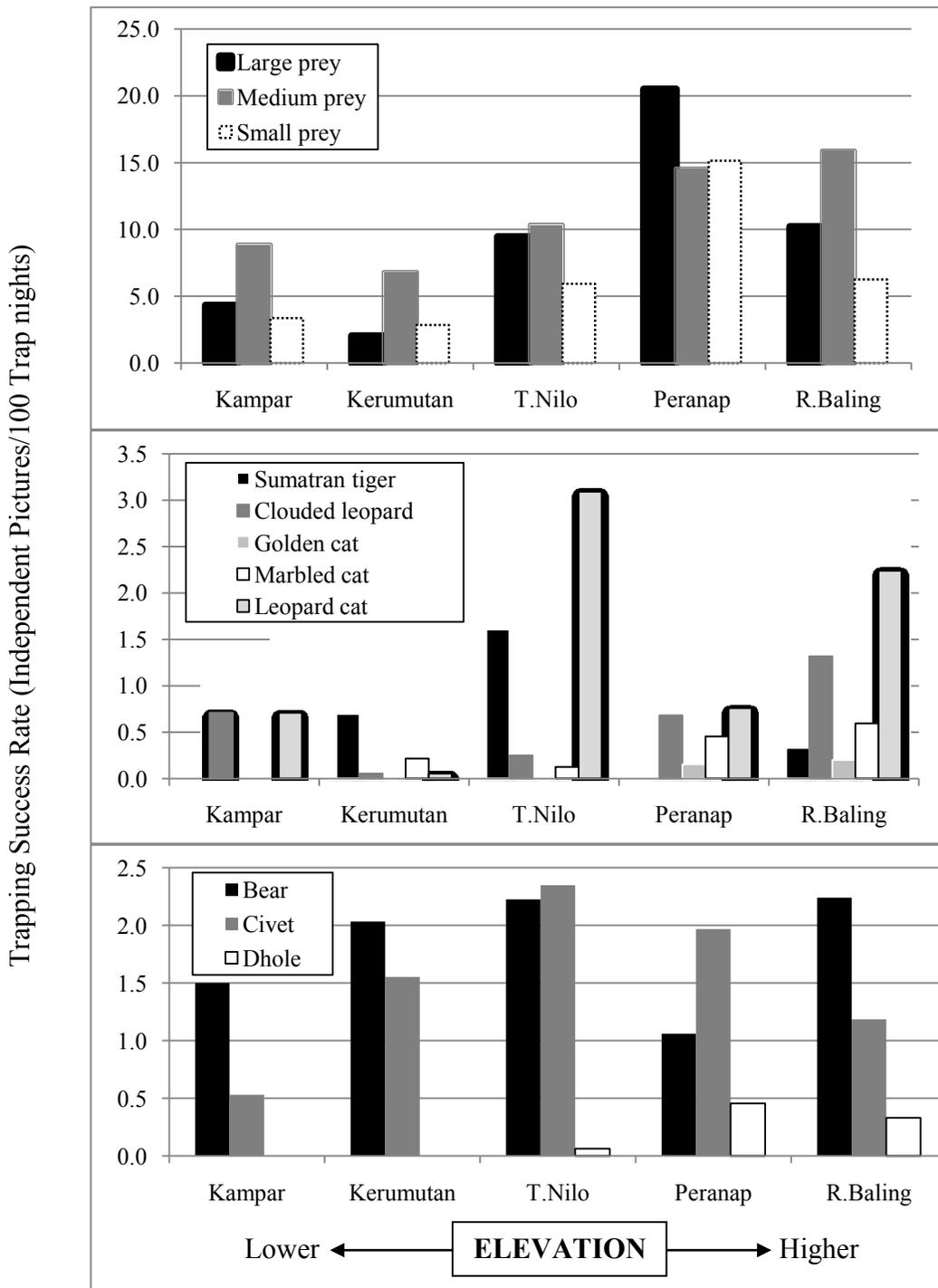


Figure 3.7. Trapping success rate for five felid species, potential prey, and other major carnivores in five forest blocks sampled.

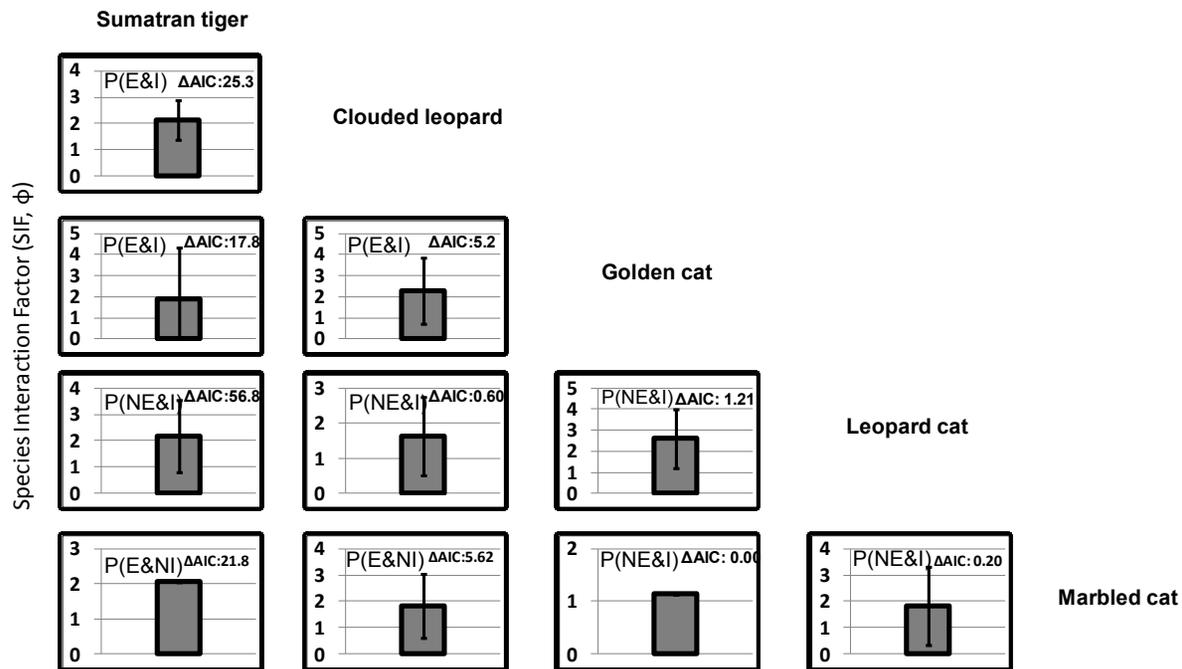


Figure 3.8. Species Interaction Factor (SIF, ϕ) between pairs of felid species based on their co-occurrence in the same camera trap stations estimated using two-species occupancy model (MacKenzie et al. 2006). SIF and SE presented were estimated from the best model from four different sets of models applied for each pair of felid. Each of the four sets of model assumes detection probability (P) as either: a) equal and independent (E&I), b) equal and non-independent (E&NE), c) non-equal and independent (NE&I), or d) non-equal and non-independent (NE&NI). Delta AIC presented is based on comparison of the models that estimate SIF and models which hold SIF constant, $\phi=1$.

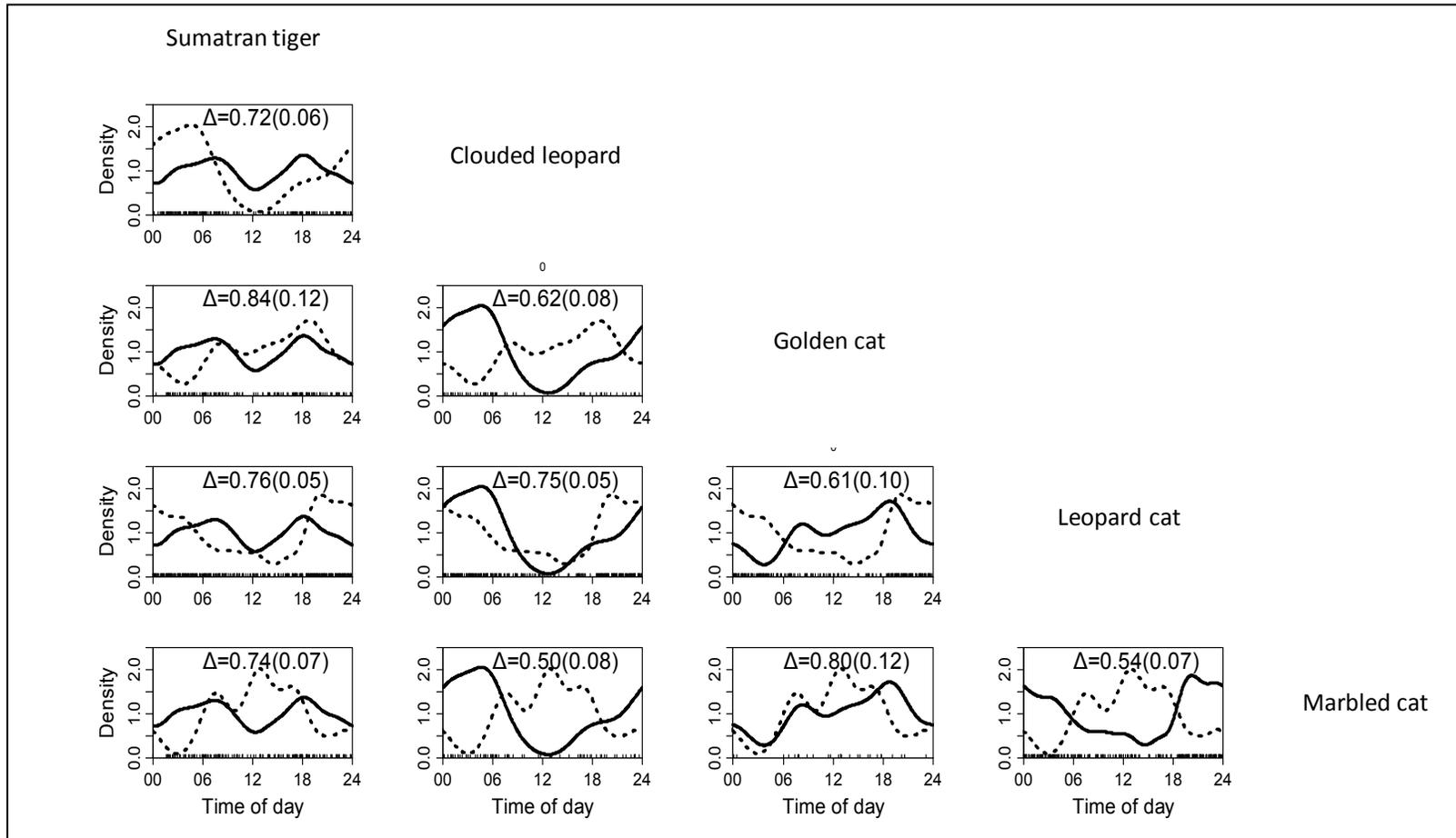


Figure 3.9. Overlap of activity patterns between felid species based on kernel density estimate on circular data. Solid lines represent species in each column, dotted lines represent species in the row. Numbers indicate coefficient of overlap, $\hat{\Delta}$ (SE).

Appendix 3.1. List of variables used to model the habitat use by felid species

No	Variable	Original Source	Treatment
1	Distance to road (“dtmprd”)	Road data from Indonesian National Mapping Agency (BAKOSURTANAL)	The original data were corrected for known errors. Distance to road raster data were derived using FindDistance in ArcView 3.2.
2	Distance to forest centroids (“dtf05cr”)	Forest-non forest classification done by WWF (Setiabudi 2006) based on satellite images acquired in 2005	Forest blocks were defined as contiguous forest area equal to or greater than 50,000 ha. Centroids of forest block were determined using ‘Generate Polygon centroid point’ in Hawth's Analysis Tools Version 3.27 (www.spataleecology.com). Distance to the Forest centroid raster data were derived using FindDistance in ArcView 3.2. Spatial Analyst.
3	Distance to forest edge (“dtfedg07”)	Forest-non forest classification done by WWF (Setiabudi 2006) based on satellite images acquired in 2007 for Central Sumatra Landscape	Using XTools version 6/1/2001 extension in ArcView 3.2, convert forest polygons to polylines (forest edge). Distance to the Forest edge raster data were derived using FindDistance in ArcView 3.2. Spatial Analyst. Values for distance-to-forest-edge were assigned to each camera trap location (buffered 500 meter) using zonal statistics ++ in Hawth's Tools
4	Distance to centroid of protected areas (“dtpacr”)	Protected area map was available from Indonesian Ministry of Forestry, maintained and updated by WWF Indonesia GIS team	Centroids of protected areas were determined using ‘Generate polygon centroid point’ in Hawth's Analysis Tools Version 3.27 (www.spataleecology.com). Distance to the Forest centroid raster data were derived using FindDistance in ArcView 3.2. Spatial Analyst.
5	Precipitation (“precip”)	Bioclim interpolated precipitation version 1.4 Release 3. http://www.worldclim.org/ (Hijmans et al. 2005),	Total annual precipitation (using raster calculator in spatial analyst, sum of 12 months’ precipitation from the original data). Data for the study area were clipped using SpatialAnalyst>Extraction>Extract by Mask.
6	Distance to fresh water (“dtwater”)	Rivers, canals, and lakes data as separate files from Digital Chart of the World Vector (line and area), downloaded through http://www.diva-gis.org/gData	Separate files were combined into one feature file in ArcGIS 9.3.1. and distance to the freshwater raster data were derived using FindDistance in ArcView 3.2.

No	Variable	Original Source	Treatment
7	Altitude ("altdem")	CIAT DEM SRTM (Shuttle Radar Topographic Mission) version 4. http://srtm.csi.cgiar.org/index.asp ; CIAT: International Center for Tropical Agriculture. These data were originally derived from USGS/NASA SRTM data (Jarvis et al. 2004).	Average altitude were calculated using Polygon in Polygon Analysis in Hawth's Tools
8	Forest area in 2007 ("for07area")	Forest-non forest classification available from WWF Indonesia (Uryu et al. 2007).	Forest areas within 500 m radii from camera station were derived using Polygon in Polygon Analysis in Hawth's Tools
9	Tree 2001 ("Tree2001")	Percent tree cover data from Global Land Cover Facility, www.landcover.org (Hansen et al. 2003, Hansen 2006)	Average number of trees was calculated using Polygon in Polygon Analysis in Hawth's Tools
10	Herb 2001 ("Herb2001")	Percent herbaceous plant cover data from Global Land Cover Facility, www.landcover.org	Average number of herbs was calculated using Polygon in Polygon Analysis in Hawth's Tools

Chapter 4

Uncertainty in predicting species distribution: a case study using four methods to map tiger occurrence in Central Sumatra

“A picture is worth a thousand words, they say, but a really good map is worth a million words” Jared Dangermond

ABSTRACT

Understanding species distribution is crucial in ecological science and wildlife management. Advancements in GIS technology, increased availability of sophisticated models, and wide accessibility to spatial data do not necessarily correspond with increased accuracy in species distribution maps. Without proper understanding, the use of sophisticated tools to develop models may even lead to more errors, increasing the uncertainty in resulting distribution maps. Few studies address this issue in species mapping. In this study, I modeled the distribution/probability of occurrence of the elusive and critically endangered Sumatran tiger in forest and plantation landscapes as a case study to illustrate the importance of accounting for uncertainty in species distribution mapping. My team and I investigated tiger presence and non-detection in 45 out of 237 possible 17x17 km grid cells in the Central Sumatra landscapes. I applied four modeling approaches differing in how the response variable (tiger presence) is constructed and used in the models. Based on the same data I arranged tiger presence into four different constructs: presence-only, presence-absence, count, and detection non-detection. Using identical predictor variables, I developed four different models respectively for the different constructs of the response variable: maximum entropy (maxent), logistic regression, zero-inflated count regression, and occupancy. I compared the performance and outputs of different models based on the relative importance of variables, descriptive statistics of the predictions, cross comparisons between models using an error matrix, and validation using tiger presence data collected from independent surveys. All models consistently identified forest area across the landscape as one of the most important variables to explain tiger probability of occurrence. Three models identified altitude as another important factor. Maxent produced the lowest estimate of tiger probability of occurrence across the landscape, followed by logistic regression and occupancy/zero-inflated regression. While the four models were generally consistent in predicting relatively high probability of tiger occurrence for high elevation forest areas such as Rimbang Baling and Bukit Tigapuluh, they had a lower level of agreement in predictions for low elevation areas, particularly the peat land in the north eastern part of the study area. Based on the results of cross evaluation of the predictions among models and validation with the independent data, I considered the occupancy model to be superior to the others. If data collection format permits, I advocate the use of occupancy instead of the other modeling techniques to develop predictive species distribution maps.

Keywords: count model, logistic regression, maximum entropy, model uncertainty, occupancy, predicting species distribution

INTRODUCTION

Understanding animal distribution not only contributes significantly to the advancement of ecological sciences (e.g., Quammen 1996, Guisan and Thuiller 2005), it also serves as an indispensable tool for effective wildlife management (Bookhout 1996, Cayuela et al. 2009) and often becomes a necessity in public policy development (e.g., Vucetich et al. 2006). To determine the status of a species and relevant management actions (e.g., Nowell and Jackson 1996, Sanderson et al. 2006, Chundawat et al. 2008), scientists and managers rely tremendously on information about the distribution of the species. Species distribution is also important to public interest because the presence of wild animals can be viewed from natural resource, environmental, educational, recreational, or safety perspectives.

Species distribution mapping is often hindered by various constraints and challenges. For instance, locational data for many species are simply lacking and occurrence of many species across their potential range is rarely known. This applies not only to species that have no direct relationship with humans, but also to those that attract public attention and are relatively well studied such as the tiger, *Panthera tigris* (Sanderson et al. 2006, Linkie and Christie 2007, Soehartono et al. 2007). Investigating species distribution through direct surveys can be expensive and there are typically very limited resources available to directly survey species occurrence across their entire distribution range. Even with direct surveys, there is still a major issue that a species might not be detected even if it is present in the site (MacKenzie 2005).

To fulfill the urgent need for species distribution maps, especially in a rapidly changing world, modeling approaches that predict the probability of occurrence of species at different scales are increasing in popularity (Guisan and Zimmermann 2000, Cayuela et al. 2009). Such

models are typically developed based on information on species occurrence as the response variable and habitat/environmental data as the predictor variables. Relationships identified between the predictor and response variables are then used to predict species probability of occurrence across the area of interest that could not be directly surveyed.

The processes and results of species distribution modeling are, however, strongly associated with various aspects of uncertainty (Couclelis 2003, Morrison et al. 2006, Dormann et al. 2008, Cayuela et al. 2009). Examples of uncertainty sources include data inaccuracies, uncertainty in variable selection, and uncertainty in model development (Guisan and Zimmermann 2000, Morrison et al. 2006). Data inaccuracies might be due to measurement error in positional and attribute data (Bolstad and Smith 1992). For species detection data there are issues such as accuracy in identification and detection probability (MacKenzie et al. 2002, MacKenzie 2005). In developing predictive models, there is always uncertainty in the selection of predictor variables to include in the model. Finally, there is also uncertainty in choice of the most appropriate modeling approach from an array of possibilities, each of which may produce different results.

Improvements in Geographical Information System (GIS) technology, availability of sophisticated models, and the availability and accessibility of spatial data required in species distribution modeling does not necessarily correspond with reduced uncertainty and increased accuracy in the resulting species distribution predictions. In fact, the risk of error in modeling may be even higher than ever before (Stauffer 2002). Therefore, the ability to measure, understand, and communicate uncertainty (Gascoigne and Wadsworth 1999) is becoming more critical. Unfortunately, few modelers address uncertainty and evaluate the accuracy in species mapping (Corsi et al. 2000).

To illustrate the importance of accounting for uncertainty in species distribution mapping, I address issues pertinent to different modeling approaches and imperfect detection of animals during field surveys. I applied four modeling approaches using identical data sets arranged in various formats according to different modeling requirements. These include modeling the species (probability of) occurrence based on presence-only, presence-absence, count, or detection-non detection data. The aims were to present, compare, and evaluate the performance and predictions resulting from the four different modeling approaches, and to compare tiger presence predictions to data collected from independent surveys as a means of model validation.

The hypothesis of this study is that different approaches will produce different depictions of tiger distribution across the landscape. Due to the simplifications and reliance on more assumptions, it is expected that predictions based on presence-only data would give the lowest estimates (underestimation) of [probability of] occurrence/distribution for tigers, followed consecutively by presence-absence, count, and detection non-detection data.

STUDY AREA

This study took place in the Central Sumatra Landscape covering a large portion of southern Riau Province and smaller parts of the bordering provinces of West Sumatra and Jambi.

Landcover in the study area consists mainly of forests and plantations. The status of the forests range from those designated to be converted, specifically for timber production, to those that are protected for the wildlife, the watershed, the ecosystem, or a combination of these features.

Plantations in the study area were dominated by oilpalm and acacia.

The landscapes have been extremely dynamic, characterized by the large-scale conversion of forests that were turned into plantations, particularly in the past 25 years (e.g., Uryu et al. 2007). This land conversion occurred due to the suitability of the geographic position and

terrain for growing oilpalm and acacia to meet the increasing global demand for pulp, paper, food, and energy. The rapid expansion of plantations that grow these commodities has been identified as the most serious threat to biological conservation of the region (Uryu et al. 2007, Gibbs et al. 2010), which is known to have extremely rich biodiversity including some of the world's most endangered wildlife species such as tigers and elephants, *Elephas maximus* (Gillison 2001, Prawiradilaga et al. 2003, Desai 2007). It is important to acknowledge, therefore, that this study depicts tiger probability of occurrence only as a snapshot from the much more complex and extremely dynamic landscape.

METHODS

Overview of the four modeling techniques

There are currently several major approaches available to predict species distribution based on the relationship between the species and the habitat or environment (Guisan and Zimmermann 2000, Cayuela et al. 2009). Species distribution can also be predicted using other techniques, including more complex modeling that takes into account beyond-habitat parameters such as migration, inter-specific interactions and so on (Guisan and Thuiller 2005). This study, however, focuses on the prediction of animal occurrence using only the habitat/environmental data as the predictor variables. I applied four approaches to model tiger distribution in Central Sumatra using the same input data, but differing in input according to the requirements of the modeling technique.

The first approach predicts species distribution across a large area based on a model developed using presence-only data as the response variable. Despite the limitations, presence records provide valuable information, particularly for rare and elusive animals (Stoms et al. 1993, Palma et al. 1999). The use of presence records to characterize habitat use and map

species distribution was reported to work for some species including Iberian lynx (*Lynx pardinus*) (Palma et al. 1999), fisher (*Martes pennanti*) (Carroll et al. 1999), great bustard (*Otis tarda*) (Osborne et al. 2001), and recently, flat-headed cats (*Prionailurus planiceps*) (Wilting et al. 2010). Using incidental sightings collected over long periods of time, Palma et al. (1999) revealed consistent association between lynx sightings and habitat features. Various computer programs have been developed to analyze presence-only data. Because it is considered robust particularly when sample size is low (Hernandez et al. 2006, Wilting et al. 2010), I used Program MaxEnt (<http://www.cs.princeton.edu/~schapire/maxent/>) in this study. It should be noted, that estimate from Program MaxEnt would be more properly regarded as an ‘index of environmental suitability’ rather than probability of occurrence for the animal. Meanwhile, pixel without species records cannot be regarded as absence in maxent prediction (Phillips et al. 2006). For the purpose of comparison with other models evaluated in this study, however, I will use the terms of ‘probability of occurrence’ and ‘probability of distribution’ to include maxent’s environmental suitability index.

The second approach models species-habitat relationships using species occurrence data that are considered as presence-absence. In this case, absence is assumed to be true absence of the target species rather than an inability to detect the species. Using logistic regression (Hosmer and Lemeshow 1989), it is possible to predict the occurrence of a species in a given area with any type of numerical data as predictor variables. It even allows re-coding a class or categorical variable into a numerical one without violating assumptions. This technique has high applicability for wildlife-habitat relationship studies as data collected from the field rarely meet with such assumptions that the other techniques (e.g., linear regression) demand. Logistic

regression can be run in commonly used statistical packages including the freely available open source R Package (R Development Core Team 2008), which I used in this study.

The third approach considers tiger occurrence as count data. In this case, instead of counts of individual animals, I used the number of transects in which tiger sign was detected within each pre-defined site or grid as the response variable. Different techniques are available to model the impacts of covariates on a count response variable. Animal count data are often problematic, however, as they typically contain excessively large number of zeros where no animals were detected in a particular survey (Sileshi 2008). This warrants the need for special models that allow appropriate statistical inference. Zero-inflated models for count data have generally addressed such an issue. In this paper, I applied zero-inflated Poisson (ZIP) and zero-inflated negative binomial (ZINB) regressions run in R software using the pscl package (<http://cran.r-project.org/web/packages/pscl/pscl.pdf>).

Finally, I used the occupancy estimation approach (MacKenzie et al. 2002, Nichols and Karanth 2002a, MacKenzie et al. 2003, MacKenzie 2005) to model the tiger's probability of occurrence. This technique also uses logistic regression models or their transformed versions (Hines 2006). Unlike other models, it incorporates the probability of detection into the estimation procedure, recognizing that detection probability is not 100% (MacKenzie and Kendall 2002). This potentially brings about a more accurate depiction of animal distribution without the need to assume that all animals present in the survey are detected (Nichols and Karanth 2002a). Although the approach was initially designed mainly to estimate site occupancy and the proportion of areas occupied by a species, it can be used to predict the geographic range and habitat characteristics of a species (Gaston and Blackburn 1996, MacKenzie et al. 2004b).

This last technique has become increasingly popular. It has been applied to the study of a variety of animal taxa for different subjects including: estimation of patch occupancy/colonization (MacKenzie et al. 2002, MacKenzie et al. 2003, Swihart et al. 2003), population/abundance (Royle and Nichols 2003, MacKenzie 2003), population viability assessment (Linkie et al. 2006), and probably most commonly for investigating wildlife-habitat relationship (Azuma et al. 1990, Ball et al. 2005, Schmidt and Pellet 2005). Models developed using this technique can be used to predict occurrence and create spatially-explicit species distribution maps, probability of occupancy/habitat use for sites that are surveyed directly or were not surveyed (Linkie et al. 2006, Karanth et al. 2009), as long as values for the same set of covariates are available from the un-surveyed sites. Given the specific data structure needs and sampling regime required for this approach, special sampling for this purpose was conducted in this study.

Field sampling for tiger data

Tiger presence, tiger ‘presence-absence’, count of the number of transects with tiger sign, and tiger detection non-detection were all generated from the same set of raw data collected with methods described in Chapter 2. The methods were developed within the occupancy survey framework (MacKenzie, Nichols et al. 2002; Nichols and Karanth 2002; MacKenzie, Nichols et al. 2003; MacKenzie 2005).

Environmental variables

To model tiger distribution, potential habitat, or probability of occurrence I used habitat and environmental variables derived from GIS data at the landscape-scale. These include 1) proportion of forest in each grid, 2) area deforested in each grid, 3) distance to forest centroid, 4)

distance to protected area centroid, 5) distance to major public road, 6) density of public roads, 7) altitude, and 8) precipitation. Explanation of how the variables were derived, the original source data, and treatments are presented in Table 4.1.

Data Input Structure

To run the analysis using different approaches, I used exactly the same sets and values of covariates, while the response variables were prepared from the same raw data into different formats. For the maxent model, only grid cells where tiger sign were detected were used to represent tiger presence records. For the logistic regression model, detection histories were collapsed further into one occasion so that each site would have a value of either 1 (tigers present) or 0 (tiger considered absent). For the count model, values for the response variable were developed based on the count of the number of sampling occasions where tigers were detected. Possible values for counts ranged from 0 to 10 (after collapsing observations from 40 transects into ten occasions, except in two sites where observations could be conducted only in 29 and 32 1-km transect respectively due to logistical constraints). For occupancy models, the response variable or detection history was developed based on detection (1) and non detection (0) data in each transect (representing a spatial replicate of the sampling occasion) within grid cells (representing sites). To create a simplified detection history, observation in 40 transects were collapsed into ten sampling replicates with, each sampling replicate represented by 4 km of consecutive transects.

Predictor variables or covariates were all first checked for correlations via a correlation matrix. If two variables were found to be highly correlated ($|r|>0.6$), only one was used for further analysis. To equalize the relative impact of variables in the model, values for each variable were normalized using z-scores where the variable's mean was subtracted from each

value of the record and divided by the variable's standard deviation. The exact same set and values of covariates were used to predict tiger distribution using the four modeling approaches.

Model development

Maxent model

I used Program MaxEnt Version 3.3.3a (Phillips et al. 2006) to predict tiger distribution in the landscape based on samples of tiger presence from the occupancy survey and environmental layers extracted in GIS. In setting up the model in Program MaxEnt, I selected the option to create a response curve of predictions showing the impact of a range of values for each variable. I also selected jackknife procedures for the program to calculate the relative importance of the predictor variables. To evaluate the performance of the model, I set the model to randomly allocate 35% of the “tiger present” samples for testing. I used 65% of the presence records as the training data on which the maxent model was developed. The rest of the options were not changed from the default. Model performance was evaluated based on the Area under the Curve (AUC) of the Receiver Operating Characteristic (ROC) of both the training and test data. AUC assessment, commonly used to deal with classification problems in machine learning and to evaluate species distribution models, produces a standardized value to evaluate model performance (Phillips et al. 2006). Tiger distribution predictions resulting from the model were then exported to ArcGIS. Probability of occurrence, which for the maxent model is appropriately called the ‘relative index of environmental suitability’ (Phillips et al. 2006), for each grid cell was then extracted using Zonal Statistic ++ under Hawth's Tool (www.spatial ecology.com) in ArcGIS for comparison with output from other models.

Logistic regression

To model tiger distribution in the landscape based on presence-absence data I used logistic regression in Program R (R Development Core Team 2008). To automatically select models based on Akaike's Information Criterion (AIC; Akaike (1973)), I used the stepAIC command with backward elimination available under the MASS package

(<http://www.stats.ox.ac.uk/pub/MASS4/>). Predictions of tiger probability of occurrence across the landscape were constructed by plugging in estimates of the regression coefficients for the applicable covariates using the logit link formula : $y = [\exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n)] / [1 + \exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_n X_n)]$; where y represents response or prediction (tiger presence); β_0 represents coefficient for the intercept; $\beta_1, \beta_2, \dots, \beta_n$ represent the estimated coefficients for predictor variables 1, 2, ... n; and X_1, X_2, \dots, X_n , represent the predictor variables (or covariate matrix).

Zero-inflated regression models

Count models were developed in Program R with the pscl package (Jackman et al. 2010). In the preliminary analysis, I developed two different count models: Zero-inflated Poisson (ZIP) and Zero-inflated Negative Binomial (ZINB). Comparison of the two models using the Vuong (1989) test did not show a significant difference between the two models (test statistic: -0.746, P=0.2278). Because it has been reported to perform better in the analysis of ecological count data (Sileshi 2008), I used the zero-inflated negative binomial (ZINB) regression model for further analysis. I used the simple version of inflation model by considering all zero counts to have the same probability of belonging to the zero components. In this case, the effect of all variables on the zero-inflation component was assumed to be constant; hence the zero-inflation model has only an intercept. This was represented in the R code as $y \sim x_1 + x_2 + \dots + x_n | 1$, where y=

response; and x_1, x_2, \dots, x_n represent predictor variables. Models were evaluated using AIC and beta coefficients from the superior model, which was used to construct the prediction of tiger distribution across the landscape based on the log link formula: $y = \exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n)$; where y represents response or prediction; β_0 represents the intercept; $\beta_1, \beta_2, \dots, \beta_n$ represent the estimated coefficients of the predictor variables 1, 2, \dots , n ; and X_1, X_2, \dots, X_n , represent the variables or matrix of covariates.

In building the model set, first I developed the constant model (without covariates). Then, I developed models that included each predictor variable in univariate form. I developed multiple variable models using combinations of covariates that, in univariate form, resulted in better model fits (relative to the constant model). The model with the lowest AIC value was considered the best, from which estimates of beta coefficients were extracted to estimate the tiger distribution across the landscape.

Occupancy

I used Program PRESENCE (Hines 2006) to estimate the probability of site occupancy (ψ or Ψ) by tigers based on the detection history data. The program recognizes the fact that not all animals present in a given site were detected and uses the detection-non-detection data to estimate detectability directly, which it then incorporates into estimates of probability of occupancy/use based on predictor variables. Using a logistic model and logit link function in Program PRESENCE, I investigated the influence of covariates on the probability of tiger occupancy for each 17x17 km grid cell. The logistic model used in the program is noted as follows (MacKenzie et al. 2006):

$$\text{logit}(\Psi_i) = \text{Ln}\left(\frac{\Psi_i}{1-\Psi_i}\right) = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_u x_{iu}$$

or,

$$\Psi_i = \frac{\exp(\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_u x_{iu})}{1 + \exp(\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_u x_{iu})}$$

where

Ψ_i = the probability of occupancy, or probability of use for i^{th} sampling unit

x_i = value for covariate measured at i^{th} sampling unit

β = regression coefficient that determines the size of the effect of the respective covariates, which are to be estimated; β_0 is the intercept term.

i = number of sampling units or sites

u = number of covariates entered into the model.

I entered data for all sites, including those directly surveyed for tiger presence and those not directly surveyed, with Ψ predicted based on covariates of the best model. In Program PRESENCE, I entered the detection history data only for sites directly surveyed and marked with a dot (.) for “missing values”, those sites not directly surveyed. In this way the model will generate individual estimates of Ψ for each grid cell that can be exported to GIS software and used to map the tiger’s probability of occurrence across the landscape.

In building the model set, first I developed the constant (no covariates) model and a constant model with autocorrelation of the spatial replicates in each cell (Hines et al. 2010). Using the model that performed best based on AIC values, I then developed models using the forest-nonforest code to model the detection probability. If adding the forest-non forest code improved the model, I then included this binary covariate for the subsequent model development.

To model the impact of covariates, I first entered each variable in univariate form. Based on the performance of the univariate models, I constructed multi-variable models using combinations of covariates to determine if model fit improved (similar to how I developed the ZINB models). I selected the best model based on AIC and used the estimates of probability of occupancy for each grid cell to construct a tiger distribution map across the landscape. I evaluated the uncertainty of the estimates based on the standard errors associated with estimate of occupancy probability for each cell.

In the resulting map depicting the probability of tiger occupancy in each grid cell across

the landscape, I highlighted unsurveyed cells that have covariate values far beyond the range observed for the surveyed cells. For example, although actual surveys were conducted in elevations from 0 to 1,250 m (measured directly in the transect), the highest average elevation of any surveyed cell was below 500 meter above sea level (based on DEM calculated in GIS); hence I had little confidence in the prediction of tiger occupancy for grids that had average elevations far beyond that range. As a warning in the interpretation, I highlighted cells in which average elevation was higher than 750 m.

Validating model output

I used several approaches to validate model output. First, the relative importance of predictor variables was evaluated based on the contribution of variables in the selected models. This was done by comparing the percent contribution of variables (for the maxent model) or examining the direction (+/-) and the value of the beta coefficient relative to its standard error. Second, the mean, minimum, maximum, and total values of model predictions were compared using descriptive statistics.

Third, I evaluated the models using an error matrix by comparing the prediction from each model against the prediction of other models as the reference, for all possible combinations. Using the method described by Jensen (1996), I calculated the omission error (predicted absent while it is present), commission error (predicted present when it is absent), overall accuracy, and a measure of agreement/accuracy based on kappa analysis ($K\text{-hat}$; Cohen 1960 , Jensen 1996). I classified the predictions of tiger probability of occurrence from all model into five categories: very low, low, medium, high, and very high. For prediction that ranged between 0 and 1, I used the same cut points generated using quantile methods in ArcGIS. With this method, output data from the occupancy model were divided into five levels of probability of tiger occupancy with

the following ranges of value: very low (0 to 0.08), low (0.08 to 0.23), medium (0.23 to 0.45), high (0.45 to 0.87), and very high (0.87 to 1). Using the same cut points, I then classified the prediction output from maxent and logistic. Model output from the count model also was classified into five categories using the quantile method. With this method, five levels of relative probability of tiger occurrence and the respective cut points from the count model were: very low (0 to 0.2379, low (0.2379 to 0.3675), medium (0.3675 to 0.6489), high (0.6489 to 1.5991), and very high (>1.5991). Error matrices were developed based on these classification categories.

Fourth, model predictions were validated using tiger presence data collected from independent surveys using camera traps and sign observations conducted in the same landscape. My team and I detected tiger presence in 20 17x17 km grid cells. These data were collected mainly to investigate tiger population size and distribution (Sunarto et al. unpublished manuscripts). I calculated the percentage of those 20 grid cells where tigers were recorded that were correctly predicted by the different models based on a series of thresholds. In this case, I did not consider non-detection as ‘absent.’ Thus, it is not possible to develop a full version of the error matrix, and I could estimate only the rate of true presence.

Lastly, four different sets of tiger distribution maps resulting from different models were presented and contrasted. Similarities and differences between the maps are discussed.

RESULTS

Comparison of model performance and relative importance of predictor variables

The four models employ different mathematical functions and procedures, hence comparison between models is not straightforward. The maxent model had relatively good fit as measured by the AUC of the ROC (Phillips et al. 2006), resulting in a value of 0.909 for the training data (scaled from 0.5 for models with no predictive ability to 1 for model with perfect prediction) and

0.742 for the test data (scaled from 0.5 for model with no predictive ability to 0.804 for model with perfect prediction; the maximum was not 1.0 because test data were taken from subset of the overall data).

The final logistic regression model, developed using backward elimination, included five variables and had an AIC of 49.49. Based on AIC weights, the final model was 13 times better in explaining the data than the full model, which included all predictor variables (Table 4.2a).

The best ZINB model included two predictor variables, forest area and altitude, to explain the probability of tiger occurrence. There were two other competing models based on delta AIC values (<2), which included the variables forest area, altitude, and road density (Table 4.2b). For simplicity and consistency with other models, further analysis was conducted using the top model with the absolute lowest AIC. In this way, instead of applying model averaging, it is possible to retain the uncertainty/standard error estimate of the prediction, especially for occupancy models, for each cell.

Occupancy models also resulted in several competing models (delta AIC <2) (Table 4.2c) with predictor variables including altitude, forest area, distance to forest centroid, and distance to protected area. I used the output from the occupancy model with the absolute lowest AIC value to map tiger distribution and for comparison with results from the other approaches. Again, by using the best model instead of the model average it is possible to present the uncertainty (i.e. standard error) of the estimates for each cell. Most of the variables in the competing models were also represented in the best model, which included three covariates for occupancy (altitude, forest area, and distance to forest centroid) and one (forest non-forest category) for the detection probability.

All models consistently identified forest area within grid cells as one of the most important variables explaining probability of tiger occurrence (Table 4.3). This variable contributed the highest percentage (59.8%) to the overall maxent model and, in all other models, had beta coefficients that were positive and relatively large compared to the standard errors, indicating that it was the most influential variable. Altitude also had relatively large and positive beta coefficients relative to the standard errors in three models. Interestingly, this variable contributed less than 1% in the maxent model. Meanwhile, road density contributed a relatively large percentage in the maxent model (14.8%), but this variable only marginally contributed to explaining tiger occurrence in two other models (logistic regression and occupancy) and did not significantly improve the explanation of probability of tiger occurrence in the count model (Table 4.3).

Assessing model output

Table 4.4 shows the summary of the overall output of the tiger occurrence predictions from four models. Three models (maxent, logistic and occupancy) produced output that was constrained between 0 and 1 (however, it should be noted that maximum for maxent output is generally below 1). In these models, tiger occurrence increased respectively from the model with presence-only data (maxent, sum=56.1, mean=0.237), presence-absence (logistic regression, sum=77.9, mean=0.329), and detection probability (occupancy, sum=100.3, mean=0.423). Output from the count model was rescaled based on quantiles as described in methods to enable comparison with other models.

The four models were consistent in assigning relatively high probability of tiger occurrence near the centroids of large forested areas, and specifically in the higher altitude areas such as Rimbang Baling and Bukit Tigapuluh (in the south and southwest of the study area)

(Figure 4.1). Larger variations in predictions were apparent for lowland areas, particularly the peatland within and around Kerumutan and Kampar (in the east and north east of the study area). Such uncertainties in predictions in those areas are particularly apparent from the relatively high standard error from occupancy models (Figure 4.4d).

Using the error matrix to assess the relative agreement of predictions among all combinations of the four models, I found that overall agreement was generally low (<60%; Table 4.5). The agreement between models was even lower based on K_{hat} estimates (the maximum being only 45%). Using the estimates of tiger occurrence from the occupancy model as the reference, I found that the count model ($K_{\text{hat}} = 45\%$) was slightly better than the logistic ($K_{\text{hat}} = 40\%$) or maxent ($K_{\text{hat}} = 23\%$) models in predicting tiger occurrence. Meanwhile, considering the other three models as the references, the occupancy model consistently had the highest level of agreement with each of the other models, and therefore considered performing better in predicting tiger occurrence relative to the other models (Table 4.5).

Validating model output against tiger presence records from independent surveys, I found that models performed differently depending on the threshold value used to consider tigers as present. The occupancy model generally performed better than other models, with the percentage of correct predictions consistently higher than other models except when the threshold was set to be high (4). However, the count model was very similar to the occupancy model and even outperformed the occupancy model at the highest (4) threshold (Figure 4.2). The logistic regression was similar to the occupancy and count models in the pattern, but produced a consistently lower rate of correct predictions for all threshold levels. The performance of the maxent model was highly variable with marked decline from low (2) to medium (3) and high (4) (Figure 4.2).

DISCUSSION

Predicting occurrence, particularly for species that are rare or elusive such as the tiger, potentially involves a large degree of uncertainty. This study demonstrates that even with the same datasets, tiger occurrence predictions can be markedly varied depending on the approach used and associated processes involved. It should be noted that this study dealt only with uncertainty pertinent to the choice of model and incorporation of detection probability. There are other potential sources of uncertainty not included in this study such as choice of variables or scales (temporal/spatial) in which studies are conducted.

Despite the uncertainty in the modeling process using the four methods, there are also similarities in the predictions. For example, areas near the forest centroids at higher altitude such as Rimbang Baling and Bukit Tigapuluh were consistently predicted to have relatively high probability of tiger occurrence. This suggests that those areas, particularly Rimbang Baling, should have better protection status and more properly managed for the conservation and management of tigers in the landscape. While the importance of the Bukit Tigapuluh area for tiger conservation has generally been recognized as a global priority for tiger conservation (Sanderson et al. 2006), this is not the case with Rimbang Baling. Bukit Tigapuluh is currently managed as a national park with relatively good financial and human resources (Franklin et al. 2004), while Rimbang Baling is badly understaffed with only three personnel with full time assignment to look after more than 100,000 ha area. Additionally, results from this study also show a large portion of potential important tiger habitats are not covered by the existing protected area system (Figure 4.1).

Conversely predictions for the peatland areas of Kerumutan and Kampar were generally not consistent among models or were associated with a high degree of uncertainty/standard error.

This suggests that the area deserves further investigation, for instance by sampling more intensively and using more specialized techniques such as using [baited] track stations (Ray and Zielinski 2008), employing detector dogs (MacKay et al. 2008), or a combination of methods (Campbell et al. 2008). In these areas, tigers have notoriously low detection probability and rarely leave observable sign due to the texture of the spongy peat substrate.

The higher probability of tiger occurrence in the western (Rimbang Baling) and southern (Bukit Tigapuluh) parts of the study area was related to the higher elevation and large portion of forest within each grid cell, variables that made a consistent contribution to most tiger occurrence models. Elevation is important in the models likely because of increased detection probability and because most lower and generally flatter forest land has already been converted into non-forest areas. Increased detectability probably results from both observers and tigers alike travelling the path of least resistance across difficult terrain and hence having a higher probability of overlap in travel paths. In higher elevation areas, only a small portion of the area is actually useable. Many areas are simply impassable due to rugged terrain. In such areas, it is typically easier to identify funnel areas where terrestrial large mammals such as the tiger would pass.

In lower elevations with more gentle terrain, all areas appear useable and natural funnel areas do not occur or are difficult to identify. Finding animal sign is even more challenging for peatland areas due to the homogenous flat terrain, and the spongy substrate preventing tracks. Additionally, scats can be easily washed out in this area due to tidal fluctuation in water levels.

In the converted lowland forest (i.e. acacia, oil palm or other types of plantations), I suspect that tigers might not be able to intensively use habitats that are more fragmented than in higher elevations. My team and I surveyed lowland forest areas and plantations and found these

areas to be associated with higher human activities and lower tiger activity (Sunarto et al. unpublished manuscript).

Comparison among models

I found the occupancy approach to be generally superior to the other three approaches. Occupancy models performed better in terms of overall accuracy and Cohen's kappa coefficient ($K\text{-hat}$; Cohen 1960, Jensen 1996), and in predicting the tiger presence for independently collected data in most threshold scenarios of tiger presence. However, the count model performed nearly as well as the occupancy model for medium or lower thresholds, and better for the high threshold in predicting sites where tigers were confirmed to be present based on independent surveys. Logistic regression appears to be biased low in predicting sites with confirmed tiger presence.

The occupancy approach has solid statistical algorithms and fewer strict assumptions regarding animal detection (MacKenzie et al. 2006). Application of this approach is also relatively straightforward with well developed publicly available software and technical support (e.g. www.phidot.org). One caveat in implementing the occupancy approach is that it requires a special data structure in the form of a detection history for each site (sample unit). This detection history can be developed in many ways. In this study I used spatial replicates to develop a detection history for each site. Detection histories can also be developed based on repeated independent visits (temporal replicates) to each site (Linkie et al. 2006), repeated assessments or questionnaires from different sources (Karanth et al. 2009), or other techniques to gain repeated measures or observations of the same event in the same site. In addition to the flexibility in choosing the survey method for the target species, the model is also flexible in allowing missing values in some of the detection history data (Hines 2006).

Due to robustness and flexibility, I believe the occupancy approach should be adopted for species-habitat modeling or distribution prediction whenever possible. Furthermore, the approach allows modelers to explicitly visualize final predictions along with the associated uncertainty for each grid cell across the landscape. The resulting maps can give better insight into areas to target for species research or conservation/management.

However, I would not recommend complete abandonment of the other approaches. For example, ZINB model performed relatively well in predicting sites with tiger presence confirmed based on independent surveys. Although logistic regression and maxent tended to underestimate the overall ‘probability of distribution/occurrence’, the general performance from this study was concordant to results of other models. I believe the performance can be improved with more presence data that are easier to obtain for this model compared to the others. The benefit of using maxent based on presence-only data, compared to the other three modeling approaches that require more information, is its flexibility to use data that simply could not be used for the other types of modeling. If such data were collected with some degree of randomness, it is likely that performance of such model can be improved in oppose to the use of occurrence data collected in ad hoc manner.

For presence-absence/logistic regression and count models, the approaches require data that, in many cases are no more complicated and might not need additional cost to obtain than detection history-type data used in occupancy model. Using either logistic regression or count models does not free modelers from assuming perfect detection probability, which is now generally recognized as a major issue in the ecological studies of animals (MacKenzie 2005). Hence, I recommend avoiding such a prevalent source of bias when an alternative is available at

little added cost. When available data allow application of only these techniques, modelers and users alike should be cautious that there might be underestimation (estimates biased low).

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Table 4.1. List and explanation of landscape variables extracted in GIS used as covariates

No	Variable	Original Source	Treatment
1	Forest area in 2007 (m ²) “for07area”	Land cover classification done by WWF (Setiabudi 2006) based on satellite images acquired in 2007 for Central Sumatra Landscape (Riau and part of Jambi Province)	Reclassified landcover types into forest-non forest; Using Grid 17, calculate the forest area (in m ²) for each grid cell using Polygon in Polygon Analysis in Hawth's Tools (http://www.spatial ecology.com/htools/polypolyanalysis.php). Average values were used.
2	Deforestation from 2006 to 2007 (m ²) “def0607area”	Forest-non forest classification done by WWF (Setiabudi 2006) based on satellite images acquired in 2006 and 2007 for Riau Province.	Deforestation or forest loss was calculated using forest cover layers from two different years (2006 and 2007, the available layers closest to the time of survey). Deforested areas were identified using Erase function in ET GeoWizard. Deforested area (in m ²) for each grid cell was calculated using Polygon in Polygon Analysis in Hawth's Tools (http://www.spatial ecology.com/htools/polypolyanalysis.php). Average values were used.
3	Distance to forest centroid (“dtf05cr”)	Forest-non forest classification done by WWF (Setiabudi 2006) based on satellite images acquired in 2005	Forest blocks were defined as contiguous forest area equal to or greater than 50,000 ha. Centroids of forest blocks were determined using 'Generate Polygon centroid point' in Hawth's Analysis Tools Version 3.27 (www.spatial ecology.com). Distance (in meter) to the Forest centroid raster data was derived using FindDistance in ArcView 3.2. Spatial Analyst.
4	Distance to centroid of protected areas (“dtpacr”)	Protected area map was available from Indonesian Ministry of Forestry, maintained and updated by WWF Indonesia GIS team	Centroids of protected areas were determined using 'Generate polygon centroid point' in Hawth's Analysis Tools Version 3.27 (www.spatial ecology.com). Distance (in meter) to the Forest centroid raster data was derived using FindDistance in ArcView 3.2. Spatial Analyst.
5	Distance to road (“dtmprd”)	Road data from Indonesian National Mapping Agency (BAKOSURTANAL)	The original data were corrected for known errors. Distance to road (in meter) raster data were derived using

Table 4.1. List and explanation of landscape variables extracted in GIS used as covariates

No	Variable	Original Source	Treatment
6	Road density (m/km ²) “densallprd”	Road data from Indonesian National Mapping Agency (BAKOSURTANAL)	FindDistance in ArcView 3.2. The original data were corrected for known errors. Road density was first derived using Line Density under ArcMap Spatial Analysis Tools. Output cell size and search radius were set to 1000 m, area unit was in sq km. This resulted in road density rasters. The value for each Grid 17x17 (m/km ²) was derived using Zonal++ in Hawth's Tools.
7	Altitude (“altdem”)	CIAT DEM SRTM (Shuttle Radar Topographic Mission) version 4. http://srtm.csi.cgiar.org/index.asp These data were originally derived from USGS/NASA SRTM data (Jarvis et al. 2004). CIAT: International Center for Tropical Agriculture	The value of average altitude for each 17x17 grid cell (m) was derived using Zonal++ in Hawth's Tools.
8	Precipitation (“precip”)	Bioclim interpolated precipitation version 1.4 Release 3. http://www.worldclim.org/ (Hijmans et al. 2005),	Total annual precipitation (in mm, using raster calculator in spatial analyst, sum of 12 months' minimum precipitation from the original data). Data for the study area were clipped using SpatialAnalyst-> Extraction -> Extract by Mask.

Tabel 4.2. AIC-based model selection and ranking for tiger occurrence across the central Sumatran landscape

a. Logistic regression

Model	AIC	Delta AIC	Model likelihood	AIC Weight	K
tigerpa ~ zfor07ar + zdensallprd + zaldem + zdtf05cr + zdtpacr	49.49	0	1.00	0.45	6
tigerpa ~ zfor07ar + zdensallprd + zaldem + zdtf05cr + zdtpacr + zprecip	51.11	1.62	0.44	0.20	7
tigerpa ~ zfor07ar + zdef0607ar + zdensallprd + zaldem + zdtf05cr + zdtpacr + zprecip	52.64	3.15	0.21	0.09	8
tigerpa ~ zfor07ar + zdef0607ar + zdensallprd + zaldem + zdtf05cr + zdtpacr + zdtmprd + zprecip	54.63	5.14	0.08	0.03	9

b. Count (ZINB)

Model	AIC	Delta AIC	Model likelihood	AIC Weight	K
tigercnt ~ zfor07ar + zaldem 1	138.42	0.00	1.00	0.445	5
tigercnt ~ zfor07ar 1	139.58	1.16	0.56	0.249	4
tigercnt ~ zfor07ar + zaldem + zdensallprd 1	140.41	1.99	0.37	0.165	6
tigercnt ~ zfor07ar + zaldem + zdensallprd + zdtpacr 1	141.89	3.47	0.18	0.079	7
tigercnt ~ zfor07ar + zaldem + zdensallprd + zdtpacr + zdtmprd 1	143.18	4.76	0.09	0.041	8
tigercnt ~ zfor07ar + zaldem + zdensallprd + zdtpacr + zdtmprd + zdtf05cr 1	145.17	6.75	0.03	0.015	9
tigercnt ~ zaldem 1	147.41	8.99	0.01	0.005	4
tigercnt ~ zdensallprd 1	151.87	13.45	0.00	0.001	4
tigercnt ~ zdtpacr 1	155.05	16.63	0.00	0.000	4
tigercnt ~ zdtmprd 1	155.10	16.68	0.00	0.000	4
tigercnt ~ zdtf05cr 1	156.05	17.63	0.00	0.000	4
tigercnt ~ . 1	156.28	17.86	0.00	0.000	3
tigercnt ~ zprecip 1	157.52	19.10	0.00	0.000	4
tigercnt ~ zdef0607ar 1	158.22	19.80	0.00	0.000	4

c. Occupancy

Model	AIC	Delta AIC	Model Likelihood	AIC weight	K
psi(zaltdem+zforest07area+zdtf05cr),thta0,thta1,p(lcfor)	318.8	0.00	1.0000	0.2272	8
psi(zaltdem+ zforest07area),thta0,thta1,p(lcfor)	318.9	0.16	0.9231	0.2097	7
psi(zaltdem),thta0,thta1,p(lcfor)	319.4	0.62	0.7334	0.1666	6
psi(zforest07area),thta0,thta1,p(lcfor)	320.5	1.72	0.4232	0.0961	6
psi(zaltdem+ zforest07area +zdtf05cr+zdtpacr),thta0,thta1,p(lcfor)	320.6	1.77	0.4127	0.0938	9
psi(zdtf05cr),thta0,thta1,p(lcfor)	321.8	3.04	0.2187	0.0497	6
psi(.),thta0,thta1,p(lcfor)	321.9	3.13	0.2091	0.0475	5
psi(zdtpacr),thta0,thta1,p(lcfor)	322.6	3.82	0.1481	0.0336	6
psi(zdef0607area),thta0,thta1,p(lcfor)	323.4	4.65	0.0978	0.0222	6
psi(zprecip),thta0,thta1,p(lcfor)	323.8	5.06	0.0797	0.0181	6
psi(zdtmprd),thta0,thta1,p(lcfor)	323.9	5.08	0.0789	0.0179	6
psi(zdensallprd),thta0,thta1,p(lcfor)	323.9	5.12	0.0773	0.0176	6
psi(.),thta0,thta1,p(.)	338.4	19.66	0.0001	0.0000	4
1 group, Constant P	345.3	26.48	0.0000	0.0000	2

Note: tigerpa= tiger presence-absence; tigercnt=count of tiger transect groups with tiger detections; psi=probability of site occupancy

by tigers; p=probability of detection; thta0 & thta1 = autocorrelation parameters; Variable names refer to Table 4.1, z in front of variable name indicates normalization of variable value with z score.

Table 4.3. Relative importance of predictor variables for tiger occurrence models from the central Sumatran landscape as indicated by the percent contribution (maxent) or estimates of beta coefficient (and standard error in brackets when applicable) from best models.

	Maxent (% contribution)	Logistic Regression (Logit link β)	Count (Log link β)	Occupancy (Logit link β)
Intercept	NA	-11.74	-2.38 (1.11)	-8.48 (4.10)
Forest area in 2007 (m ²) (“zfor07area”)	59.8	1.30	0.73 (0.22)	0.61 (0.50)
Deforestation from 2006 to 2007 (m ²) (“zdef0607area”)	1.7	NA	NA	NA
Distance to forest centroids (“zdtf05cr”)	0.1	-0.77	NA	-0.85 (0.66)
Distance to centroid of protected areas (“zdtpacr”)	8.8	-1.07	NA	NA
Distance to road (“zdtmprd”)	12.5	NA	NA	NA
Road density (m/km ²) “zdensallprd”	14.8	0.92	NA	0.05 (0.69)
Altitude (“zaltdem”)	0.7	113.09	20.94 (11.79)	94.08 (45.55)
Precipitation (“zprecip”)	1.7	NA	NA	NA

Table 4.4. Summary of the output values of tiger occurrence predictions from the four models of tiger presence in central Sumatra.

	Maxent*)	Logistic	Count	Occupancy
Minimum	0	0	0	0
Maximum	0.9	1	128.3	1.0
Aggregate (sum from all cells)	56.1	77.9	482.6	100.3
Mean	0.237	0.329	2.036	0.423
Standard Error	0.013	0.025	0.595	0.023
Coefficient of Variation	0.871	1.185	4.499	0.830

*) Maxent prediction should be considered as an ‘index of environmental suitability’

Table 4.5. Summary results of model agreement based on cross-evaluation of tiger occurrence, considering the result of each model as the “truth” (columns) predicted respectively by the other models (rows).

	Probability of tiger occurrence ⇕	REFERENCE															
		Maxent				Logistic				Count				Occupancy			
		Error of omission	Error of commission	Overall agreement	K-hat	Error of omission	Error of commission	Overall agreement	K-hat	Error of omission	Error of commission	Overall agreement	K-hat	Error of omission	Error of commission	Overall agreement	K-hat
Maxent	VL					29	73	28	13	55	58	38	22	47	51	38	23
	L					46	12			73	36			71	35		
	M					45	18			32	27			36	29		
	H					38	31			24	31			34	46		
	VH					2	100			2	100			2	100		
Logistic	VL	73	29	28	13					96	39	47	34	100	43	52	40
	L	12	46			14	27	10	19								
	M	18	45			17	36	9	18								
	H	31	38			33	52	49	79								
	VH	100	2			77	82	90	96								
Count	VL	58	55	38	22	39	96	47	34					73	77	56	45
	L	36	73			27	14			45	45						
	M	27	32			36	17			36	34						
	H	31	24			52	33			43	43						
	VH	100	2			82	77			79	79						
Occupancy	VL	51	47	38	23	43	100	52	40	77	73	56	45				
	L	35	71			19	10			45	45						
	M	29	36			18	9			34	36						
	H	46	34			79	49			43	43						
	VH	100	2			96	90			79	79						

Note: unit for every number is percent; Omission error= predicted absent while it is present, Commission error = predicted present when it is absent; categories of tiger occurrence prediction: VL=very low, L=low, M=medium, H=High, VH=Very high (See text for detailed method).

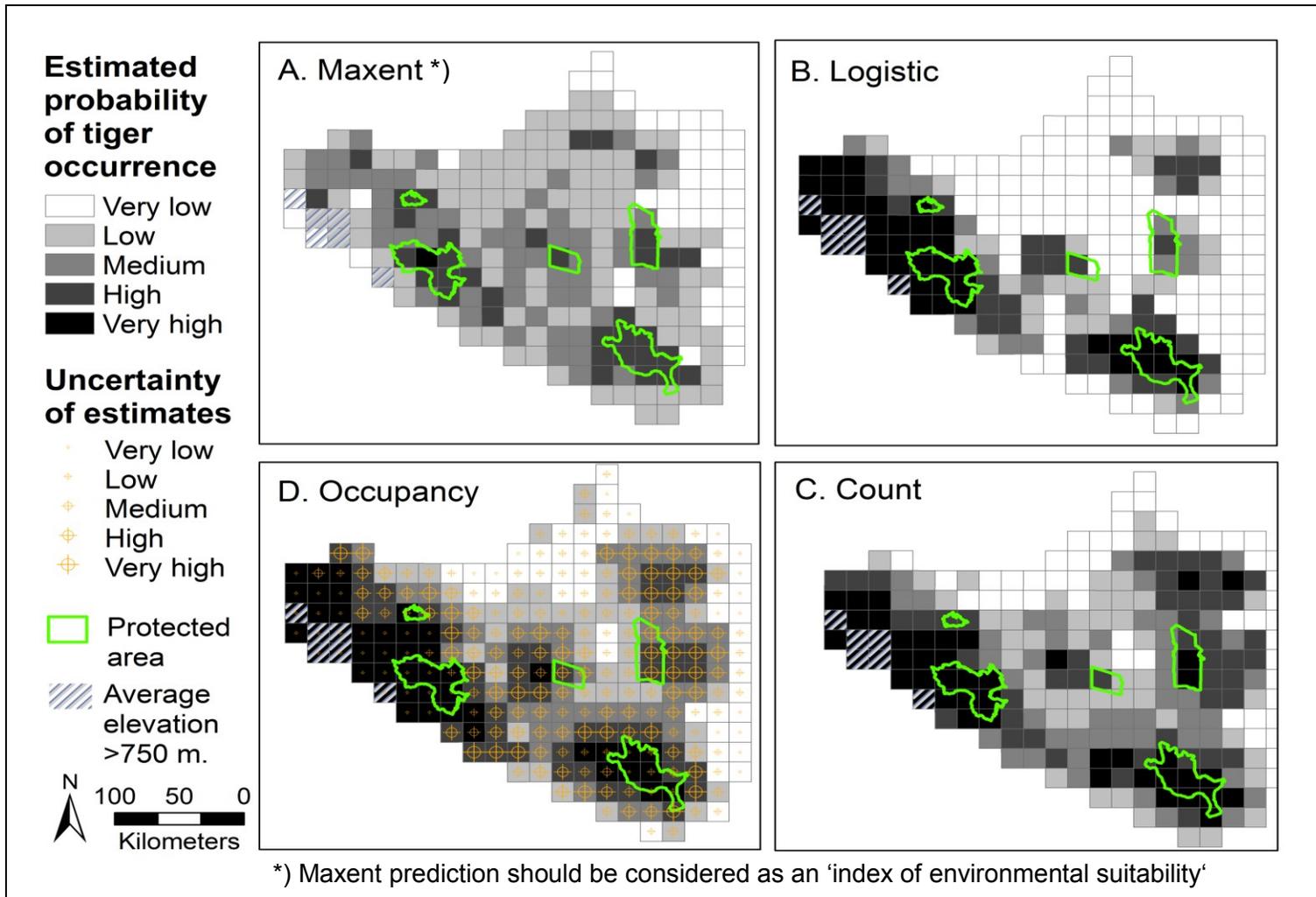


Figure 4.1. Probability of tiger occurrence in the study area as predicted using four different models. Note: See text for detailed methods including the cut points used to determine the tiger occurrence probability categories.

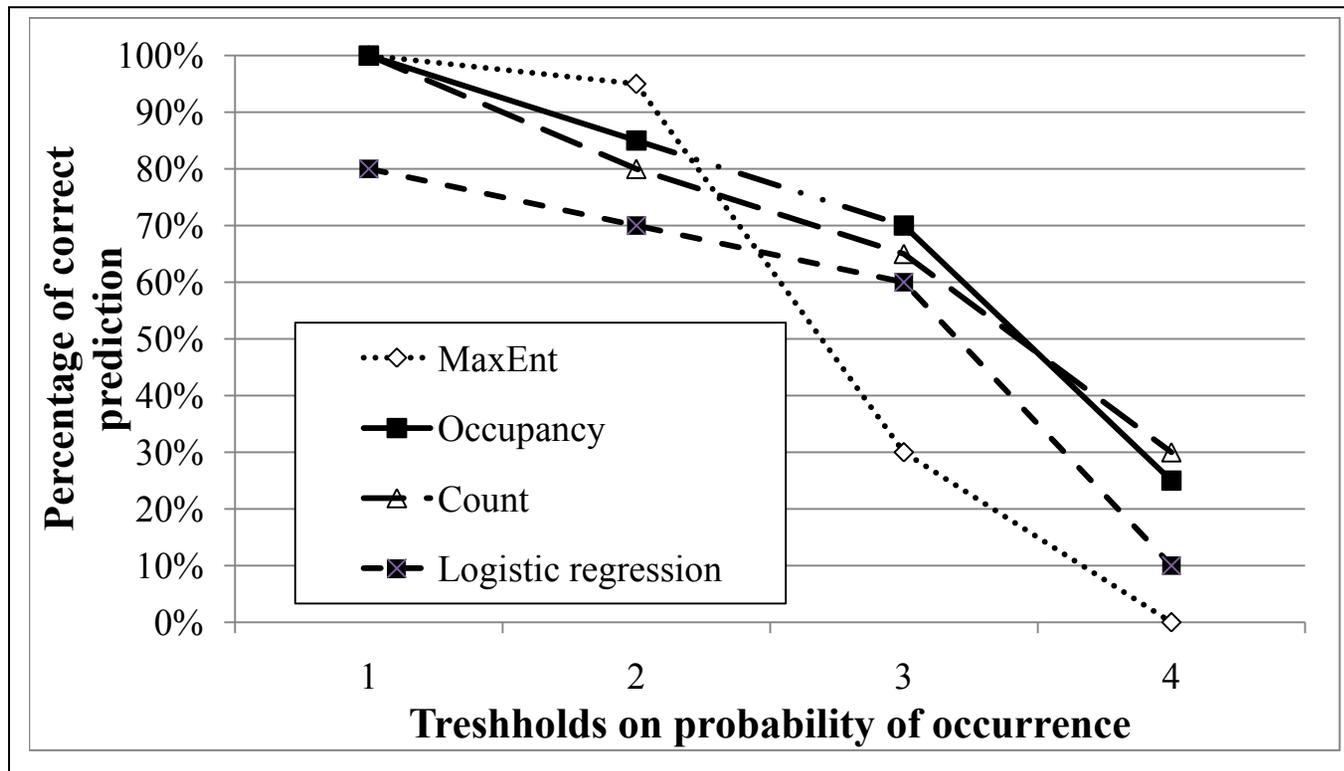


Figure 4.2. Comparison of model performance in predicting tiger presence: percentage of correctly predicted present sites for grid cells where tigers were detected in independent surveys (n=20 grid cells) based on different probability of occurrence thresholds.

Note: Threshold of probability from maxent, logistic, and occupancy model outputs to classify as presence: 1=very low (>0.08), 2=low (>0.23), 3= medium (>0.45), 4= high (>0.87); Thresholds for the count model were determined based on 5 classes of count response identified using Quantile methods in ArcGIS: 1= very low (>0.2379), 2= low (>0.3675), 3=medium (>0.6489), 4=high (>1.5991).

Chapter 5

Repaint the stripes: a strategy for the restoration of tigers and the ecosystem in the Central Sumatran Landscape

“The goal is to give wildlife and human communities alike the best chance to adapt and survive in a changing landscape.” Douglas H. Chadwick

ABSTRACT

This paper presents a strategy to restore the tiger population across the ecosystem of Central Sumatra through integration of information on tiger ecology presented in the previous chapters with consideration on the ecological conditions of the landscape. The strategy combines existing knowledge of tiger conservation and regional ecosystem restoration. It formulates a landscape-scale vision to conserve tigers in core areas and to restore connectivity between subpopulations. The vision recognizes the limitations and challenges of traditional nature protection and considers the existing and new opportunities. Emerging opportunities and new mechanisms, such as direct and indirect economic incentives for nature conservation and restoration, are taken into account. These, coupled with increased awareness of the stakeholders, better policies and implementation of good governance, and the willingness and know-how to maintain coexistence with wildlife among the locals, are expected to support and accelerate the recovery of tigers and their ecosystem.

Keywords: carnivore restoration, connectivity, core habitat, corridor, habitat mosaic, human-carnivore coexistence, landscape zoning, multi-use landscape, stepping stone.

Background

Known as the stronghold for the Sumatran tiger population (Borner 1978), Riau Province in Central Sumatra has undergone massive change characterized by large-scale deforestation and conversion of forests into plantations (Uryu et al. 2007). In addition to losing their habitats, tigers in the landscape suffer from direct killing in the form of poaching to supply the black market with tiger body parts (Shepherd and Magnus 2004) or in retaliation due to conflict with humans (Nyhus and Tilson 2004).

Large-scale conversions and degradation of forests in the landscape not only have disrupted the ecosystem, but have also threatened the tiger specifically, and biodiversity in

general. Some of the sites known to hold some of the highest plant diversity on the planet (Gillison 2001) have been destroyed or badly degraded (Holden 2002). Populations of the Asian elephant have been extirpated from several patches in the landscape (Desai 2007). As wildlife loses habitat, more frequent encounters with people lead to increased conflicts between humans and wildlife (especially tigers or elephants), resulting in casualties to both parties (WWF 2008).

Overexploitation and mismanagement of the natural resources in the landscape have caused people to suffer from associated disasters such as floods and fires. Such adversities often took place in this impoverished ecosystem, impacting not only the local, but also regional people.

Tigers in the landscape

Despite this bleak picture, landscapes in southern Riau still contain some natural areas that can potentially be restored to create a multi-use landscape. My team and I have gathered encouraging evidence with regard to tigers that casts new hope for their conservation in the landscape. For example, my surveys found that tigers were still roaming in every major forest block within the study area in the southern part of the province. My team and I found that tigers not only could live in undisturbed forests, but also used secondary or degraded forests, and occasionally roamed into some plantation areas.

My investigations have revealed some ecological realities of the tiger in Southern Riau that were previously unknown. For example, the tiger abundance study found that different habitat/forest types in the landscape do not hold equivalent numbers of tigers per unit area. Meanwhile, within specific locations such as in Tesso Nilo, tiger abundance fluctuated through time, and was potentially increasing. I identified factors such as prey availability, understory

vegetation cover, and level of human activity as possible determinants of the variations in tiger abundance.

Compared to other areas in the tiger's range, I found that tiger densities in Central Sumatra were very low. In some forest areas, tigers were so rare that more than a thousand days of camera trapping recorded no pictures of tigers despite their confirmed presence based on their pugmarks. This low density means that each of the forest blocks in the landscape is inhabited by a small number of tigers that, without conservation intervention, are unlikely to survive over the long term. To ensure their long-term viability, therefore, establishing connectivity between habitats and subpopulations is crucial in addition to direct protection of tigers and habitats in the core areas.

My tiger occupancy study revealed that habitat selection depended on the spatial scale of analysis. At the landscape scale, the selection of home ranges by individual tigers (second-order selection; Johnson 1980) was associated with higher altitude and proximity to the centroid of large forest blocks. While within their home range, tigers selected areas with thicker understory cover and higher altitude and avoided areas associated with high levels of human activity (settlements). Understory cover and human disturbance appears related directly to the ecological requirements of the tiger, while higher altitude could be confounded with factors such as larger proportion of forest (important factor for tiger home range selection), terrain steepness (causing higher detections of tiger sign), or lower level of human disturbance (preferred by tigers).

Tigers varied in their preference for habitat conditions within different land cover types. For example, within forest areas tigers occupied sites that were farther from water (possibly due to the higher human activity often focused around rivers), and had thicker understory cover (thought to be effective for stalking, hunting and hiding from humans). Tigers significantly

avoided sites with high human disturbance especially in the forms of encroachment and settlement. In contrast, within acacia plantations, tigers preferred sites that were closer to water (presumably associated with the protection of vegetation ‘greenbelts’ along riverbanks in the plantation concession). They preferred sites with higher level/risk of encroachment, which were typically areas with less maintenance, older plants, and more leaf litter. They avoided sites with higher levels of logging activity and tended to avoid sites with higher levels of human activity and steeper slope. Tigers tended to use older plantations (for acacia) and younger (for oilpalm), both of which had higher plant diversity and particularly for acacia, relatively lower levels of human activity.

Despite tiger presence within and around plantations, human-tiger conflicts involving industrial plantation workers were relatively rare. Some companies even recorded zero conflict with tigers during their many years of operation despite the companies’ location directly bordering tiger habitat. Years of tiger study in oilpalm plantation concessions in Jambi, Sumatra documented at least 16 tigers roamed within and around the concession (Maddox et al. 2007), yet never recorded any conflict incidents despite high levels of human activity in the same areas as indicated by the high human photo-capture rate (1,413 non-researcher human photos out of 6,286 pictures) documented from camera traps (D. Priatna/ZSL, personal communication). Out of 149 conflict incidences recorded from 2001 to 2007 in Riau, the majority (~35%) took place in the forest where victims were mostly conducting (illegal) activities such as logging, hunting, or fishing (WWF unpublished data). Conflicts taking place outside of the forest were typically due to depredation of livestock by tigers, or attacks by tigers on individual farmers working or resting solitarily in or nearby recently opened forest areas. Most of the conflict in the province

(~67%) took place in the intertidal peatland areas of Dumai and Rokan Hilir Regencies, which are outside of the landscape of this study.

With adjustments in the plantation management, tigers could use mosaics of habitat in plantation areas that had adequate understory cover and low levels of human activity as additional roaming zones, riparian forests as corridors, and smaller forest patches as stepping stones to travel between main habitat patches across the forest and plantation landscapes.

Restoration of tigers and the ecosystem

Ecosystem health is one of the most fundamental components of human well-being (Haines-Young and Potschin 2010, Reyers et al. 2010, White et al. 2010). In impoverished ecosystems, the importance of restoring large mammals to improve ecosystem health has been relatively well documented (Noss 2001). Tigers, like other large top predators, have an essential role in the natural process to maintain ecosystem health (Terborgh et al. 1999). The loss of top predators not only affects prey animals, but potentially could trigger a series of detrimental events known as a trophic cascade (McLaren and Peterson 1994, Crooks and Soule 1999, Ripple et al. 2001, Terborgh et al. 2001, Terborgh and Estes 2010). Although the mechanisms are not always easy to study, particularly in terrestrial ecosystems, the extinction of top predators may lead to species extinction or decreasing prey biodiversity (Paine 1966), and bring ecosystems into a more simplified form (Terborgh et al. 1999, Rawinski 2008). For example, the extirpation of predators in the eastern US have led the white-tailed deer (*Odocoileus virginianus*) to become overabundant, particularly in suburbia and parks where hunting is prohibited (McShea et al. 1997, Terborgh et al. 1999, Rawinski 2008), causing the extirpation or prevention of growth of many rare plant species (Rawinski 2008).

To restore the tiger population and ensure its long-term viability, two major steps are required. First, the critical core areas should be conserved (Walston et al. 2010). Second, more areas should be protected and restored, especially those that connect subpopulations (Wikramanayake et al. 2010). These steps can only be achieved and maintained over the long-term if stakeholders are convinced that benefits of tiger restoration (economically and socially) outweigh benefits of activities that threaten the animals and their habitats.

Restoring tigers in the landscape at this scale, with the associated ecological and sociological complexities, is certainly not an easy undertaking. The sooner the effort starts, however, the easier and less expensive it should be. Waiting longer with the ongoing environmental degradation may result in key areas becoming completely devastated. These areas could become source populations for re-colonization of floral and faunal species. Restoration should be relatively easier than reintroduction, which is what will be required if the tiger becomes completely extirpated from the landscape. At this time, and at least in most places in the landscape (compared to those in other landscapes where tigers have long been extirpated), people still generally have a relatively high degree of acceptance of the native animals, including tigers. Additionally, independent efforts to conserve some of the natural areas are already underway in the landscape. Current studies in the landscape (e.g. previous chapters) have shown that tigers can use plantation areas between core habitats. Meanwhile, some plantation companies have demonstrated their interest and commitment to supporting conservation. With a clearer vision, future efforts to conserve and restore the natural areas in the landscape can be better coordinated.

The key to begin a more concerted restoration effort is to define a clear vision (Terborgh and Soulé 1999, Mansourian et al. 2005, Sumardi et al. 2009), followed by outlining the required steps of actions and detailing the appropriate methods. While the vision is defined at the larger

landscapes, the actions can be implemented at a local scale, moving toward achieving the larger vision.

The use of tigers as the focal species for the integral restoration of the ecosystem has many reasons and benefits. Tigers are not only highly respected in the traditional cultures in Sumatra, but also attract public attention around the globe. Therefore, tigers play a role as a flagship species in conservation to gather support from wider communities (Linkie and Christie 2007). As an animal with large home range that can occupy virtually any natural area in Sumatra, the tiger can also be considered as an umbrella species such that protection of this species with its large area requirements results in vast biodiversity protection. In addition, studies have recognized the central role of apex predators as keystone species in controlling prey numbers (e.g., Paine 1966, Terborgh et al. 2001, Sinclair et al. 2003) or prey behavior, especially relative to predation avoidance, such as herd/flock formation, guarding, and alarm calling (Terborgh 1990, Terborgh et al. 1999). Although generalizing impacts remains controversial, removal of predators also may have further consequences that can cascade through ecosystems (Terborgh et al. 1999, Terborgh et al. 2001).

To thrive, the tiger needs food, cover, space to roam, mates, and protection from killing. The requirements for tiger survival in the landscape over the long term can be viewed as complementing, rather than competing with, the human need for a healthy ecosystem. With such a premise, in the next sections this paper presents a bold vision and subsequent strategies for the restoration of tigers and the ecosystem. The strategies will include a descriptive account of the conditions needed to achieve success, identification of ways to achieve these conditions, recognition of challenges, and highlights of the opportunities and reasons for optimism.

Restoration vision

I begin by identifying tiger conservation zones in the landscape (Figure 5.1). This restoration vision was constructed based on the ecological needs of the tiger over the long term. It is integrated with ecosystem ‘functions’ and ‘services’ for the people (Costanza et al. 1997, Reyers et al. 2010), designed to preserve the vertical (across different trophic levels) and horizontal (across spatial patches) flows of energy and materials (Risser. 1990). This representation of critical elements of the ecosystem includes variation in habitat type and landscape features (Noss et al. 1999), and conservation of evolutionary processes (Maehr 2001), which are important considerations in the construction of the vision. To construct the spatial vision, first I take into account the current conditions based on the predicted probabilities of tiger occupancy across the landscape from the best occupancy model as presented in the previous chapter.

In the spatial vision, using a similar approach as in the restoration of the eastern timber wolf (Eastern Timber Wolf Recovery Team 1992), I classified the overall landscape into four different zones. I first identified the “core zone”, the highest priority zone for tiger conservation, from the clusters of areas with highest probability of tiger occupancy. Because of the generally low probability of occupancy (with high uncertainty) in the peatland areas, I considered clusters of cells with the highest categories of probability of occupancy in the area as the core zones. A small cluster of core zones identified from the model, such as Tesso Nilo, that contains only three 17x17-km grid cells, was expanded in the vision to include four grid cells – which require habitat restoration - to allow the accommodation of higher numbers of tiger individuals. Neighboring core zones are connected to each other by extension zone and/or integrated zones. “Extension Zones are defined as transitional areas surrounding core zones with relatively lower probability of tiger occurrence. “Integrated Zones” are areas with even lower probability of tiger

occurrence and/or those with relatively high intensity of human activity. Areas that do not fall within one of those criteria were classified as “least concern”.

The goal to achieve in the future is projected from current conditions, and the need for habitat that potentially can support tigers, in terms of numbers and configuration of the (sub)populations, to survive in the long term. Due to the fragmentation of the natural forest in the landscape and the small number of individuals inhabiting each core area, I must consider maintaining and restoring the connectivity between sub-populations (Anderson and Jenkins 2006) to maintain meta-population structure (Gotelli 2001), allowing gene flow and ‘rescue-effects’ to operate. Because it proved challenging to obtain precise tiger population estimates in low density areas (Chapter 1), level of occupancy might be used as proxy indicator for the population.

The goal is to maintain or increase the overall level of tiger occupancy across the landscape. The current aggregate probability of occupancy (if all values added together) for 237 cells in the landscape is 100.3, with probability in every cell ranging from 0 to 1, and average probability of occupancy per cell of 0.423. This aggregate probability of occupancy, which can be considered equivalent to total population size of the tiger in the landscape (Boyce and McDonald 1999), can be used as the baseline in population monitoring to measure the effectiveness of management interventions. The management target for each cell in the core zone, for example, can be set to maintain at least medium level (≥ 0.50 , for peatland) and high level (≥ 0.75 , for mineral soil) of tiger probability of occupancy. Also important for the long-term goal is to improve the configuration of tiger occupied areas from current condition, allowing movements of tiger individuals and gene flow between core areas or subpopulations. Some areas I identified as ‘least concern’ currently contributed to the aggregate occupancy

figure, in the future can be assumed to have zero probability of occupancy. To increase or at least stabilize the level of aggregate probability of occupancy across the landscape, therefore, will require compensation of increased levels of occupancy from areas identified as either core, extension or integrated zones.

Connectivity and synchronization of this vision to the other landscapes at the larger scale were also considered. For example, to the southwest, the landscape can potentially be connected with the larger Kerinci Seblat Landscape; to the northeast with Giam-Siak-Kecil and further to Senepis; and to the northwest with Rimbo-Panti (Figure 5.3).

Expected conditions and restoration objectives within the key zones

Projected general conditions to achieve for each zone are summarized in Table V.1. In the vision map, I identified five clusters of tiger conservation core zones. Two core zones, Kampar Peninsula and Kerumutan, represent peat swamp forest type that is very distinct in comparison to other areas. Tesso Nilo (TN) core zone represents flat-dry lowland forest, while the rest of the zones including Bukit Tigapuluh (BT), and Rimbang Baling-Bukit Bungkok- Hulu Kampar Kanan (RBBBHKK) mostly represent hill forests in the higher elevation with little to no relatively-flat lowland forest.

Each core zone is expected to be a self-sustained ecosystem that can support a tiger population for an extended period of time, ~25 years with no or minimal management intervention. In the monitoring program, this can be indicated for example by stable or increased level of occupancy across cells in the areas identified as the core zones. For the longer-term and particularly when conditions change (e.g., due to climate change), each core area will benefit from the neighboring core area through connectivity and the network of metapopulation structure.

I envision that tigers breed within each of these core zones. To allow such a condition to take place, an adequate amount and quality of prey animals must be available. Maintaining high habitat quality and low disturbance from human activities in these zones should ensure adequate prey availability and mating opportunities for tigers. This will require strict protection. Although slight modifications of habitat for enrichment purposes might be conducted, other modifications should not be permitted. All core zones must, therefore, have legal protection. Noss et al. (1999) provide further a detailed account of the concept of core areas including their significance in large-scale restoration and conservation efforts, their purpose from various perspectives, and how to manage them.

Currently, several areas identified as core areas in the landscape are lacking protection status. These include the majority of the Kampar Peninsula, the eastern part of Kerumutan Wildlife Reserve, the periphery of Bukit Tigapuluh National Park, the periphery of Rimbang Baling and its adjoining areas ensuring connectivity to Bukit Bungkuk and Hulu Kampar-Kanan.

Core zones *per se* are often too small to support adequate numbers of tigers to maintain viability over the long term. Meanwhile, individual core areas can also be easily threatened as the environment, or orientation of regional development, changes. Extension zones are required and thus identified here. These zones can serve as habitat extensions of the core zones providing a buffer from unwanted disturbances and providing connectivity with other core zones. In addition, the extension zones may function as a filter or buffer, for example to reduce the adverse impacts of human activities and to reduce the risk of human-wildlife conflicts.

From development perspective, extension zones can be managed for limited human use as long as the functions of supporting the core zone and/or providing connectivity to other core zones can be maintained. Although strict protection might not be required in this zone, some

critical areas such as those directly bordering core zones, or those that are identified to be critical corridors or stepping stones for tiger movements, such as those between Kerumutan and Kampar, should be permanently protected. Because of the nature of the multiple-use extension zones, these areas might become the most likely interface between tigers and humans. We, therefore, should anticipate human-tiger conflict, take actions to prevent conflict, and plan for conflict mitigation - including proper response when conflict occurs. Typical land use in extension zones might include protection forest (mainly for watershed protection), limited production forests, or high conservation value areas within plantation concessions.

Integrated zones are crucial for the long-term viability of the tiger, other species, and overall biodiversity conservation across the fragmented landscape. Incorporation of the integrated zones in the overall landscape restoration program is expected to benefit both wildlife and human society. Integrated zones are specifically managed human use areas that allow connectivity and flow of energy and materials within the ecosystem framework between core zones. Successful restoration of the integrated zones will have an impact by restoring connectivity between the otherwise isolated populations of flora and fauna in the core zones. Connectivity also ensures the flow of environmental services that nature provides (Soule and Terborgh 1999). The benefits for humans may include cleaner air, better oxygen and water supply, buffers from natural disasters such as typhoons, landslides, floods, etc., increased recreational and tourism opportunities, and a generally healthier environment (Costanza et al. 1997).

Compared to the core and extension zones, I expect much lower tiger use of the integrated zone. In some areas, it might take years after the neighboring areas are restored, before these zones become useable as wildlife movement corridors. However, since human density is

likely higher in integrated than in core or extension zones, efforts to anticipate, avoid and mitigate human-wildlife conflict (for example by regulating farming and livestock husbandry activities, implementing insurance and compensation mechanisms) should become an integral part of the restoration programs.

How to achieve the objectives

Achieving the objectives of tiger and ecosystem restoration in the landscape requires a simultaneous combination of programs and actions (Table V.2) involving individuals in the landscape and wider members of regional and global community. Protection of the core zones requires strong advocacy from civil society, political will, and long-term commitment from the government. Meanwhile, the role of civil societies nationally and internationally is also crucial. Through national and international organizations, communities from outside of the region can potentially provide funding that is required to manage the core areas. In some cases, local people may be required to give up their land and some economic development activities, bearing the cost of restoration for which they may deserve compensation. Wider communities, particularly those that derive benefits from the restored landscape, are obligated to provide economic and other forms of incentives to the local stakeholders to conserve the natural habitats.

Protection of extension zones rests on the long-term commitment and day-to-day involvement of the private sectors that typically manage forest or plantation concessions in the landscape. Incentives (e.g., premium prices of green products) and disincentives (pressures or punishments) from government, markets, and civil society are required to promote the adoption and implementation of better management practices (BMP) in this sector. Support, appreciation/encouragement, and enforcement from governments are keys for the continued and successful implementation of the BMP principles.

Restoration of the integrated zones will require involvement of more parties at a relatively smaller scale yet widespread in occurrence. Integrated zones can be utilized by a range of landowners ranging from small-holder farmers, suburban households, to large companies operating in various sectors. Although not all of these parties are required to share habitat with wildlife, their support for ecosystem restoration and their willingness to coexist with tigers and other wildlife potentially ranging in their neighborhoods are crucial.

Restoration efforts will only become effective if good governance and enabling socio-economic climates exist. Creating a favorable environment for restoration activities requires major changes in a number of government policies beginning with a change in the economic development strategies (from short-term-oriented extraction-based to more sustainable use of resources). Such strategies should be reflected in a revised spatial and development plan at various levels (national/island, provincial, regency, sub-regency, village, individual land owners) with stronger emphasis on overall ecosystem health, not short-term economic indicators to measure success. Meanwhile, many laws and regulations, particularly those having conflicting interests among agencies/sectors, likely require revision or adjustment, and once approved, should be strictly and consistently enforced.

A legitimate coordinating body will be required to provide direction, to ensure that restoration efforts are organized and synchronized. It should include monitoring and evaluation, as well as technical assistance in the implementation of ecosystem restoration. The organizational form of such a body is to be defined democratically involving key stakeholders. Further refinement of the restoration strategy is needed to translate the landscape-scale vision into smaller scale objectives, programs, and actions that should take place at different scales from the smallest possible management units across the landscape. Among other tasks, this body

is to make sure that a variety of management activities are simultaneously and continuously undertaken in synergy across different zones (Table V.2).

Priority actions

Actions required to achieve the objectives described above should take place simultaneously across geographic locations at different scales. Due to limited resources, however, prioritization is required. Highest priority actions should be based on their relative importance and urgency, taking into account the probability of success considering the opportunities and challenges. I consider conservation of the existing natural areas to be less expensive and more practical, ecologically and socially, than restoring areas that are already degraded or totally devastated. Therefore, protection of the existing natural habitats will generally be considered as the highest priority restoration action.

Protecting the remaining natural areas

The overlay between the core zone and the existing protected areas shows that some core zones lack legal protection status either partially or totally (Figure 5.1). Many of these areas still contain relatively large portions of natural forest. These include all areas in Kampar Peninsula, the area to the east of Kerumutan Wildlife Reserve, the surrounding area mainly to the west of Bukit Tigapuluh National Park, the area around Rimbang Baling Wildlife Reserve, particularly that connecting to Bukit Bungkuk Nature Reserve, and the area in the Hulu Kampar-Kanan.

Once legally protected, it would possibly be more efficient if these five clusters of core zones could be managed by four, instead of five, management units. Each unit could focus on one or more core area cluster(s) that has/have a distinct habitat type or geographic position: first for the peatland area of Kerumutan-Kampar (as an extension or upgrade from the existing

Kerumutan Wildlife Reserve), second and third respectively for BT and TN National Parks (existing management units), and fourth for the RBBBHKK.

Another high priority action would be to protect the remaining natural forest within the extension and integrated zones allowing some limited use in the extension zones. Natural forests are still relatively large within some extension zones, particularly in Kampar Peninsula, the eastern part of Kerumutan, the western part of Bukit Tigapuluh, and the surroundings of Rimbang Baling all the way to Hulu Kampar-Kanan.

In addition, protection for the remaining natural forests within the integrated zones should become a high priority. The patches of forest, although relatively small in size, can potentially play crucial roles as stepping stones for individual tigers, or other wildlife, on the move. The forest patches can also become the backbone for further restoration of landscape connectivity or wildlife corridors. Hence, such patches likely have disproportionately high value relative to their size. Forests in integrated zones, as they are typically surrounded by a sea of developed areas, are even more vulnerable than those located within core or extension zones. Thus, level of urgency is probably the highest to protect these scattered natural areas.

Large portion of the landscape, including forest areas outside of the major protected areas, mostly are already allocated for agricultural or timber concessions (Figure 5.2). Further and more detailed evaluations are necessary to determine future management status and to make sure that they are synchronized with the long-term vision to restore the tiger.

Improving the effectiveness of protected area management

Legal, on-paper protection of areas in the landscape is not necessarily followed by regulated access or intensive patrolling to prevent illegal activities from taking place within the park's boundary. In some areas, protected area boundaries are still not clearly demarcated and often are

disputed in the field. Conservation area management activities, including enforcement, in the majority of the protected areas in the landscape are also badly understaffed and underfunded. An example is the 136,000 ha Rimbang Baling Wildlife Reserve that is looked after by only three full time staff with barely any facilities to patrol or conduct typical activities for park management. Improvement in protected area management is urgent and crucial particularly for Rimbang Baling and Kerumutan. Crucial activities required include habitat protection, anti-poaching patrols and enforcement, and restoration of degraded areas within the protected areas.

Outreach and mitigation of human-wildlife conflict

Unmitigated and poorly handled conflicts between wildlife and people not only have claimed many casualties from both sides, they have directly contributed to the declines in endangered species such as tigers and elephants. Conflicts also become one of the most prominent sources of public resentment for wildlife conservation. Educating people about how to prevent and avoid conflict with wildlife, equipping them with the necessary knowledge and infrastructure to mitigate conflict, and professionally handling conflict incidents are crucial for tiger conservation. Furthermore, as public support is extremely important for successful restoration efforts, it should be promoted through strategic and continuing outreach programs highlighting the importance of nature and wildlife conservation. Outreach programs can be more effective if there is a clear, direct link with incentive and disincentive mechanisms. People who demonstrate better behavior and take supportive actions toward conservation should receive incentives, those who bear the burden such as loss of livestock or giving up economic opportunities should receive adequate compensation.

Improving policies needed for the restoration

Adoption and implementation of restoration programs by targeted stakeholders require a supportive political climate and policies. One of the most crucial policies would be the adoption of the proposed tiger spatial conservation vision into various levels of the government's landscape plans. Meanwhile, mechanisms to promote incentives for protection and restoration of natural areas also require supporting policies developed by governments and organizations of various private sectors and civil societies.

Monitoring and investigation

Restoration programs should be informed and developed based on rigorous scientific works and solid monitoring programs conducted in the context of adaptive management (O'Connor et al. 2005, Nichols and Williams 2006). At this stage, principles in tiger and ecosystem restoration are generally known, while data and knowledge required in decision making are available to take action. Therefore, it is not necessary to wait until more data become available to take action.

Tiger population monitoring in the context of adaptive management needed to answer specific management questions should be integrated in overall and every step of restoration activities. Effectiveness of the impacts of different management programs or restoration activities should be measured on the change in tiger abundance or occupancy. Changes in the overall level of occupancy across the landscape, as well as on specific target areas, should be documented and compared between those areas receiving different management interventions. This can be conducted, for example, by estimating tiger abundance/density in some select locations on a yearly basis and by assessing the changes of the level of tiger occupancy across the landscape and in selected areas every other year. Such programs to monitor tiger population parameters should be closely linked with measurable management interventions, for example,

the effort to promote tiger habitat/population connectivity between certain critical areas. Every restoration program should be evaluated to assess its impact and effectiveness.

Although current state of knowledge on tigers and general landscape condition is sufficient to commence the tiger restoration program in the landscape, further actions will likely require more detailed, advanced and up-to-date information on the ecological aspects of tigers in the landscape. Various aspects of the ecology and behavior of tigers, such as their ranging behavior, particularly in the matrix of non-natural habitats, are still yet to be revealed. The sensitivity/tolerance of tigers to different types of human activities also warrants further investigation.

Challenges

Major tasks and challenges to achieve restoration objectives lie in the realm of human dimensions. While tiger conservation receives great support from wider communities, local stakeholders hold the keys to successful coexistence with tigers and to sustainable ecosystem restoration. Challenges to tiger restoration in the landscapes can be classified into several categories. First, a relatively large portion of the country's population is still living beneath the poverty line. The region is undergoing rapid economic development and desperately trying to improve the prosperity of the people, making the challenge to conservation even larger. Forest lands identified as important for tiger conservation, are targets of extraction, conversion, and other development activities. Many people need jobs. Therefore, it is crucial that conservation and restoration programs promote sustainable economic development, job creation, and opportunities for income generation, particularly for the local communities.

People living in the tiger landscapes will need the support from wider communities to conserve and restore the tiger because threats to tigers in the landscape are mostly caused by

external sources. For example, large-scale extraction of natural resources that caused the shrinkage of tiger habitats was mainly due to external factors such as the demand for food, consumer products, and sources of energy (Uryu et al. 2007, Koh and Ghazoul 2008, WWF et al. 2008). As a consequence, current land use largely reflects the development of the area to supply the regional or global demands for such commodities.

The second challenge to tiger conservation lies with socio-psychological factors. The tiger has complex dimensions, not only ecologically but also socially and culturally. Unlike other animals, the tiger cannot be understood merely using ordinary ecological sciences (Seidensticker et al. 1999b). That is especially relevant in Sumatra and other Malay regions, where the myths and metaphysical aspects often prevail over the state of the art of ecological knowledge of this species (Seidensticker et al. 1999b, Boomgaard 2001). For example traditional people in some areas in Sumatra that harbor tigers, also believe in the ‘weretiger’, a supernatural being that can transform interchangeably into human and tiger (Boomgaard 2001). While such a belief system has discouraged some people from attacking tigers (Boomgaard 2001), it also led to persecution of tigers or other animals (e.g., Jno 2010).

Due to their unique characteristics, conservation of tigers receives extremely strong support, but also creates strong resentment. Consistent with general findings from previous studies that show greater support for environmental protection comes from urban communities (e.g.,Lowe et al. 1980, Van Liere and Dunlap 1980, but see also Williams Jr. and Moorey 1991), my experience suggests that the strongest supporters of tiger conservation are typically urban people or those from other countries who have little or no experience living in the tiger landscapes. Meanwhile, based on visits to several villages in the landscape, I found that those who value tigers in the wild were typically elderly people from more traditional villages, who are

declining in number. In many places in Sumatra, particularly in the focus area of this study, most people in the villages, especially young people, have become modernized and practiced few of traditional lifestyles. As a consequence, traditional values including respect for nature are declining. While many have left their traditional practices, they are not necessarily exposed to, let alone embracing, modern ecological sciences. The challenge will be to formulate an approach with stakeholders who are in a cultural transitional stage.

The last challenge is ecological. Although generally less complicated than the human-dimensions described above, many ecological challenges in tiger conservation remain unresolved. Despite the rapid progress in ecological sciences revealing the ecological requirements for tiger survival, there are aspects that remain unresolved, especially in Sumatra where tigers generally live in dense forest at very low density. Most tiger studies in Sumatra are still dealing with basic aspects of tiger ecology, mainly focusing on abundance estimation in a few sampling blocks. Tiger behavior, ranging patterns, social interactions, population dynamics (fecundity, survival etc), role in ecosystems, intra-specific interactions, interactions with prey, and interactions with humans remain poorly studied or totally unexplored in Sumatra. An understanding of such tiger ecological aspects is important for effective management and restoration of this species.

Opportunities and optimism

The restoration vision and goals formulated in this exercise may sound ambitious; however, there are reasons to be optimistic that they are achievable. There are success stories for large mammal conservations programs from many places that can be used as a model. In addition, in Sumatra there have been recent changes in attitude and behavior of some key stakeholders, changes in economic and development policies at the national and global level, new opportunities and

mechanisms for nature conservation that are recently available, and many other positive developments pertinent to conservation.

Globally, examples of successful restoration of wildlife are available from a number of places. In the US for example, several species have been brought back from the brink of extinction or local extirpation to relatively secure conditions. These include the recovery of the bald eagle, *Haliaeetus leucocephalus* (American Eagle Foundation 2007), California condor, *Gymnogyps californianus* (Walters et al. 2010), American elk, *Cervus canadensis* (Cooperative Conservation America 2010), American bison, *Bison bison* (Gates et al. 2010), American alligator, *Alligator mississippiensis* (Savannah River Ecology Laboratory 2010), grey wolf, *Canis lupus* (Fritts et al. 2001), and grizzly bear, *Ursus arctos* (Office of Public Affairs 2007). The fundamental similarity between these animals and the Sumatran tiger is that, when they were in their worst condition, most people were skeptical that restoration would be successful. From some standpoints, the situation with tigers in Central Sumatra Landscape is still better than most of those species when they were in their worst conditions.

Examples of successful conservation or recovery of wildlife species are also available from countries in regions facing economic and political challenges, such as Africa with the recovery of the African elephants, *Loxodonta africana* (Blanc 2008) and Asia for tigers. Success stories of tiger conservation have been reported from Kaziranga (Ahmed et al. 2010) and the Terai Arc Landscape (Dinerstein et al. 2007). Meanwhile, tiger life history characteristics are another reason for optimism. Characterized by high reproductive rate (Sunquist et al. 1999), tigers are able to bounce back from pressure to their population as long as habitat and an adequate amount of prey are available (Karanth and Smith 1999, Sunquist et al. 1999, Karanth et

al. 2006), and level of human disturbance is minimized (Griffith and van Schaik 1993, Harihar et al. 2009, Sunarto et al. 2010a).

Positive progress in conservation has also been made in Indonesia, where many new protected areas have been added in the past few decades. This includes the legal protection of some critical tiger habitat areas in Sumatra. Some examples include the protection of Bukit Tigapuluh (2002), Batang Gadis (2004), and Tesso Nilo National Parks (2004 for first establishment, 2009 for expansion). The first and the last previously bore production forest status. The protection of these areas has set new examples contrary to the common practice of forest conversion following the extraction of timber from natural forest. In addition, a new and encouraging regulation (Government Decree No 6/2007) has been issued that allows companies to hold a forest concession for ecosystem restoration instead of for logging. Harapan Rainforest, an ex-logging concession located in Jambi Province bought out by conservation groups for ecosystem restoration, has become the first case for this new initiative (BirdLife 2008) and so far appears to be showing some indications of success.

The last few years also have seen some progress with regard to the commitment of the government for development activities that take the environment into account. For example, governors in Sumatra have recently signed an agreement to adopt an ecosystem-based spatial plan (<http://news.mongabay.com/2008/1008-sumatra.html>). Government agencies, along with civil societies, are in the process of following up this high-level commitment to implement real action in the field. In addition, recent ecological disasters including floods/landslides, land fires, and consequently the haze, have raised questions, if not to say awareness, among some members of communities that I met about the importance of forest and natural area conservation. This should be seen as an opportunity to further raise the issue.

Globally, increased concern for the impact of climate change has translated into a better political climate and policies more conducive to promoting conservation and restoration through mechanisms such as co-benefit of the protection of natural areas and restoration of the degraded lands. Direct co-payment for the protection or restoration of forests that serve as carbon storage and sequestration can potentially provide funding for conservation management and prevent conversion of the natural forest into palm oil plantations (Venter et al. 2009). Furthermore, increased awareness and pressures from consumers of agricultural and forestry products originating in Sumatra, have brought about some changes in the behavior of the private sectors in conducting business.

Finally, to specifically address the crisis related to the decline in tigers and their habitat, several international movements are underway. These include high level government advocacy conducted under name of the Global Tiger Initiatives (<http://www.globaltigerinitiative.org/>) that have recently organized the Global Tiger Summit achieving a landmark commitment to double the tiger population across the range countries within a decade (Global Tiger Recovery Program 2010b;a). Additionally, major NGOs such as Wildlife Conservation Society, Panthera, and World Wildlife Fund are also running large-scale tiger-specific conservation programs; Tigers Forever (<http://www.panthera.org/programs/tiger/tigers-forever>) and Tiger Network Initiative (<http://wwf.panda.org/>). These likely will bring further positive change among the stakeholders. If key stakeholders can be convinced and examples demonstrated that restoration of tigers and the ecosystem bring benefits to them, establishing landscapes where tigers thrive along with society is not merely an ecological utopia, but a practical and achievable goal.

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Table 5.1. Expected general condition in each tiger conservation zone for tiger and ecosystem restoration in Central Sumatra Landscapes

	Core	Extension	Integrated	Least Concern
Expected status	Strict protection (e.g., core zone of national park, wildlife reserve, nature reserve)	Conservation with limited use	Integrated between development and protection of critical areas for possible movement	No protection specifically for tigers is required
Action needed	Total protection or, if in degraded condition, restoration into habitable areas for tigers and prey	Protection or, for degraded habitat in critical areas, restoration to allow use by tigers and prey	Promoting uses that will improve habitat value for tigers and prey, particularly for areas critical for tiger movement	NA
Conflict avoidance, mitigation and resolution	Tiger highly prioritized, human activities should strictly consider tiger activities	Tigers likely use this area, human activities should assume that	The area is likely used by tigers, critical areas within the grid should be identified and human activities are accordingly regulated	NA
Expected habitat conditions	Nearly 100% suitable and self-sustained habitat conditions that support different activities of tigers including hunting for prey, mating and breeding.	Areas are habitable by tigers, particularly those bordering the core zone and critical linkages with other core zone	Tigers and other animals have room to pass this zone without conflict with human	NA
Expected prey conditions	Prey animals are abundant across the zone.	Prey animals are relatively high, particularly in	Prey animals are available in designated areas	NA

	Core	Extension	Integrated	Least Concern
	Hunting strictly prohibited	areas bordering with the core zone. Hunting generally prohibited		
Human presence and activities	Strictly limited. No permanent settlement allowed within the zone	Strictly regulated. Permanent settlement should be minimized. Human activities limited in certain areas and/or times that will not disturb tiger activities	Regulated in critical areas within the zone	Centers of human activities

Table 5.2. Suggested relative intensity of key management activities in different zones for tiger and ecosystem restoration in Central Sumatra Landscapes. Note: More checks (✓) indicate higher intensity.

Key management activities	Core	Extension	Integrated	Least concern
Ecological research	✓✓	✓✓	✓✓	-
Habitat management and restoration	✓✓	✓✓✓	✓✓	-
Protection	✓✓✓	✓✓	✓	-
Awareness & education	✓	✓✓	✓✓✓	✓✓
Policy work	✓	✓✓	✓	-

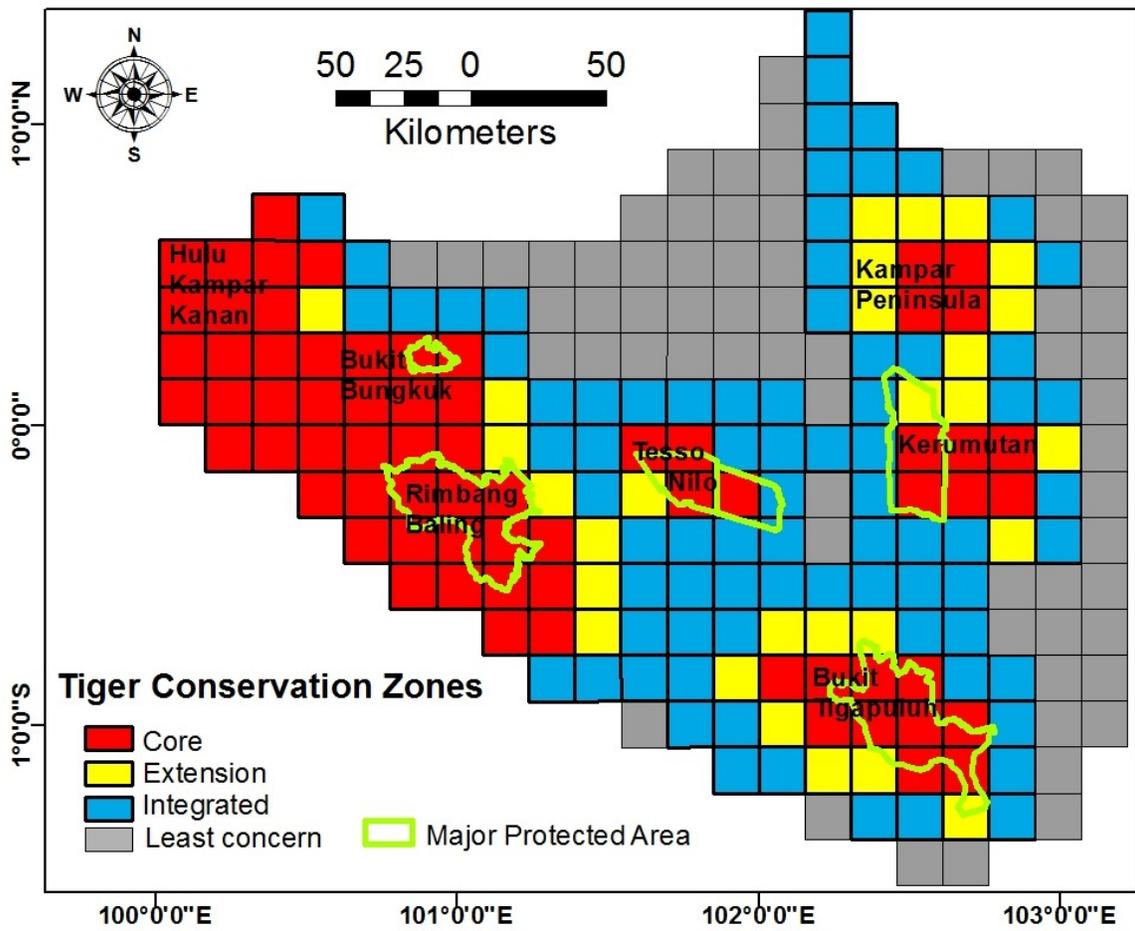


Figure 5.1. Spatial vision for tiger and ecosystem restoration in the Central Sumatra Landscapes.

Note: each square represents 17x17-km grid cell.

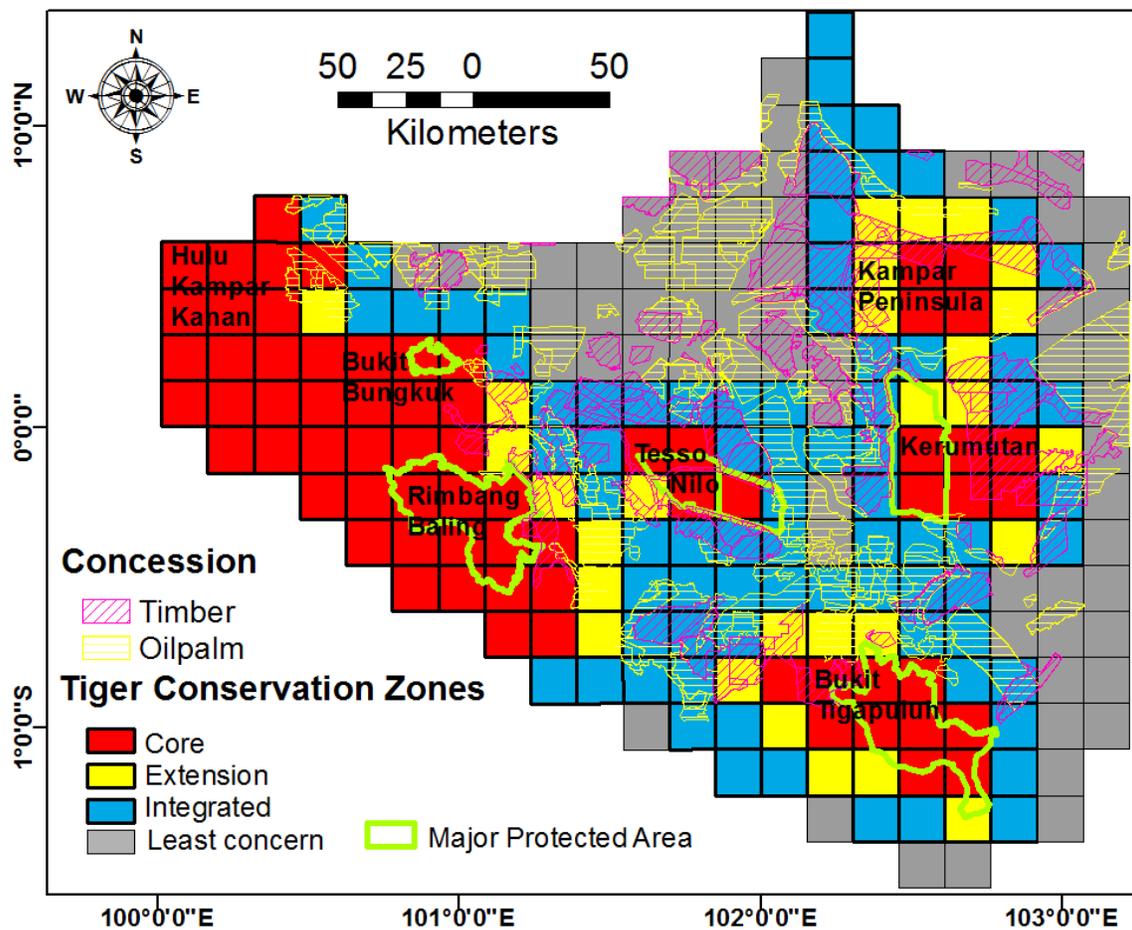


Figure 5.2. Existing concessions for timber (based on 2006 data) and oilpalm (based on 2004 data) in the landscape superimposed on the spatial vision for tiger and ecosystem restoration in the Central Sumatra Landscapes.

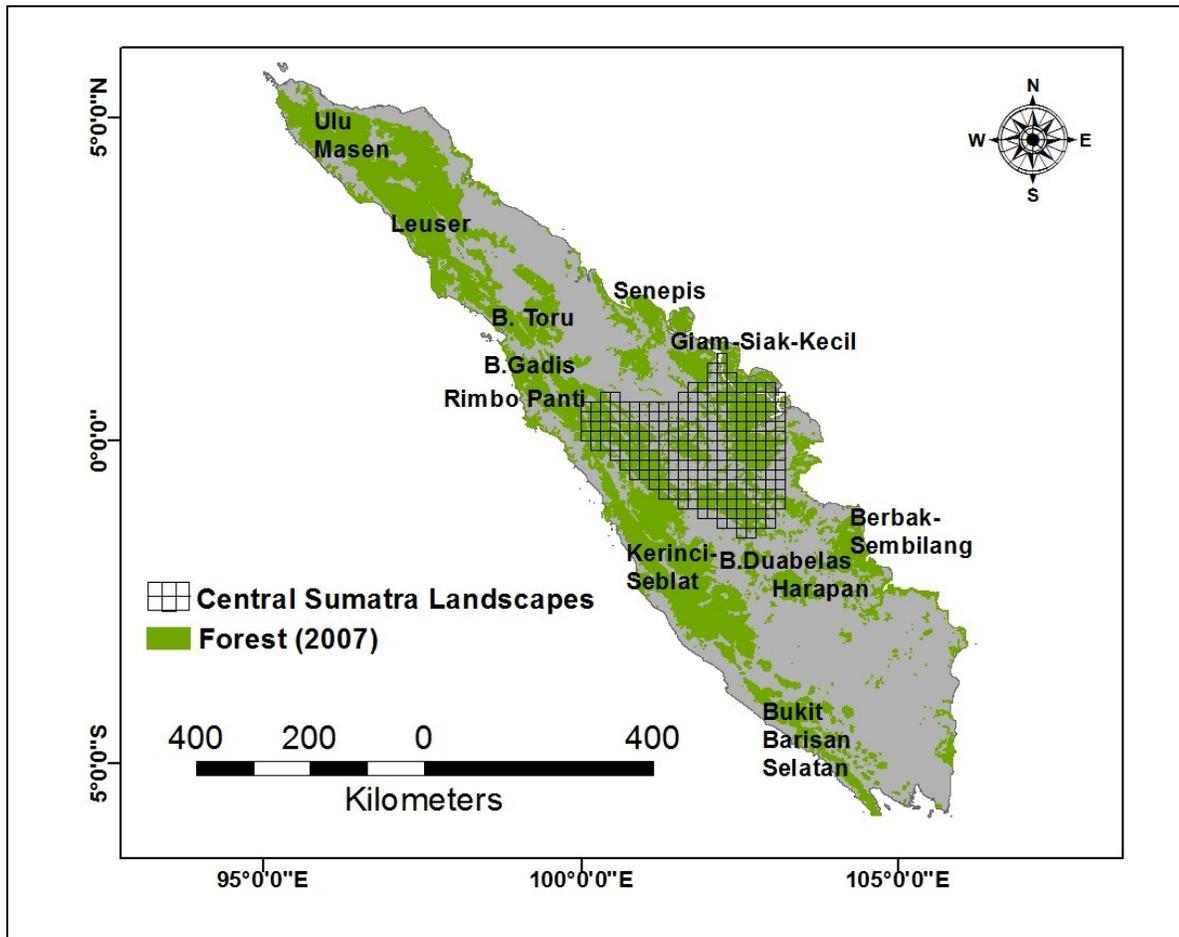


Figure 5.3. Potential connectivity between Central Sumatra Landscapes and other tiger landscapes in Sumatra. Note: each square in Central Sumatra Landscape represents 17x17-km grid cell.