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An Individual-based Model Approach for the Conservation of the Sumatran Tiger *Panthera tigris sumatrae* Population in Central Sumatra

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Summary

This dissertation demonstrates the construction of the Panthera Population Persistence (PPP), an individual-based model for the Sumatran tiger (*Panthera tigris sumatrae*) which provides proper theoretical and application frameworks for the conservation of this tiger sub-species in central Sumatra. The PPP model was developed to gain insight into tiger-prey-habitat relationships as well as the effect of human impacts on the persistence of tiger populations. The model addresses three main problems for the survival of the Sumatran tiger: tiger poaching, prey depletion, and habitat loss.

The description of the PPP model serves as an in-depth study of existing literature and covers the most important factors of existing models for tiger conservation. Existing modelling approaches have been improved by the inclusion of finer description of individual-level traits and behaviours in the PPP model. The modelling approach allows a direct inter-relationships between individuals and their environment. The relationship between individual behaviours, intrinsic states, and external factors are simulated spatially explicitly in a bottom-up approach where the emergence of the population dynamics of tiger and prey can be observed under different scenarios. The integration between the PPP model and geographical information system (GIS) has provided a much more meaningful spatial data by revealing the mechanism of the response of individuals to the present land-use types.

The relative importance of the parameters within the PPP model was tested using two modes of sensitivity analysis: The Morris Method and the traditional One-factor-at-a-time method. The results provided guidance for the application of reasonable sensitivity analysis during the devel-

opment of individual-based models. The Morris Method suggested that the overall output of the PPP model showed a high sensitivity on the change of time required by a tigress to take care of cubs. The analysis also revealed that the number of dispersers was sensitive toward perceptual distance of individuals to detect the presence of prey. Comparison with a similar predator-prey models provided insight into the predator-prey relationship. The comparison also suggested that perceptual distance of the individual is important for any spatially explicit individual-based model involving predator-prey relationships. The parameterization of the individual perceptual distance of tigers was tested by using existing literature on prey consumption by tigers as a benchmark. The simulation results were within the range of scientific acceptance for the number of prey killed by a tiger. Thus, further use of the set of parameters for a tiger's perceptual distance is less uncertain for the output of the PPP model.

The effect of habitat quality and landscape configuration on the mortality and migration of prey were evaluated through the use of virtual habitats and landscapes. The findings suggested that a good habitat quality enables prey survival, increases the population available for predation by tigers. When a low-quality habitat is combined with a high-quality habitat, the number of migrating prey was high, reducing resources for tigers. This suggested that landscape composition should be considered when predicting population persistence of the Sumatran tiger. Optimal movement of two different prey resulted in a high density of prey in high-quality habitat, providing a concentration of prey in a tiger's habitat, but resulted in a lower tiger predation rate than random movement and species specific movement.

The PPP model has been applied to evaluate the effect of poaching, prey depletion, and their combination for the probability of extinction of a tiger population. The results from the evaluation showed that prey depletion, tiger poaching, and a combination of both, created a 100% probability of extinction within 20 years if the density and frequency of those threats at high rates. However, the duration of those threats in the system caused a 100% probability of extinction from tiger poaching. The results are able to contribute to optimize anti-poaching programs in future, to reduce significantly the probability of total extinction of Sumatran tiger.

Furthermore, various landscape configurations have been tested against the probability and time of extinction for the Sumatran tiger population. The integration of spatial GIS-data in the model provides an insight into the relationship between tiger-prey-habitat. The results suggested that habitat quality surrounding a protected area plays an important role for the persistence of the Sumatran tiger population. This study also recommends agroforestry systems as reasonable land-use type in the vicinity of protected areas. They provide not only positive effects for tiger conservation purpose but they also appear as adaptable to the current land-use situation in Sumatra island.

Zusammenfassung

Die vorliegende Dissertation beschreibt die Entwicklung des Panthera Populations Persistence (PPP) Modells, eines individuenbasierten Simulationsmodells für den Sumatra-Tiger (*Panthera tigris sumatrae*). Dieses stellt einen geeigneten theoretischen und anwendungsbezogenen Rahmen für den Schutz dieser Tiger-Unterart in Zentralsumatra bereit. Das PPP-Modell wurde entwickelt, um Einblicke in die Tiger-Beute-Habitat-Beziehungen zu gewinnen, sowie um den Effekt anthropogener Einflüsse auf den Fortbestand von Tigerpopulationen abzuschätzen. Dabei werden die drei Hauptprobleme für das Überleben des Sumatra-Tigers analysiert: die Wilderei, der Rückgang von Beutetieren und der Verlust von geeigneten Habitaten.

Die Beschreibung des PPP-Modells gibt zunächst einen umfassenden Überblick zum aktuellen Wissensstand auf dem Gebiet des Tigerschutzes und integriert die wichtigsten Faktoren bereits existierender Modellansätze. Diese konnten durch die Einbeziehung einer detaillierten Beschreibung von individuellen Merkmalen und Verhalten verbessert werden. Das PPP-Modell stellt somit das Individuum in einen direkten Zusammenhang mit dessen Umwelt. Die Beziehung zwischen individuellem Verhalten, intrinsischen Merkmalen und externen Faktoren werden räumlich-explizit in einem bottom-up Ansatz simuliert. Damit kann sowohl die Populationsdynamik des Tigers als auch die seiner Beutetiere unter verschiedenen Annahmen beobachtet werden. Die Verknüpfung des PPP-Modells mit Geographischen Informationssystemen (GIS) bietet die Möglichkeit, die Reaktionsmechanismen der Individuen basierend auf der gegenwärtigen Landnutzungssituation zu simulieren und somit realitätsnahe räumliche Daten zu generieren.

Die relative Bedeutung der Modell-Parameter auf die Simulationsergebnisse kann durch Sensitivitätsanalysen ermittelt werden. Hier wurden zwei verschiedene Ansätze verwendet: die Morris-Methode und die herkömmliche One-factor-at-a-time Methode. Der Vergleich beider methodischen Ansätze zeigte somit beispielhaft die Eignung unterschiedlicher Sensitivitätsanalysen für individuenbasierte Modelle auf. Die Morris-Methode zeigte, dass das Gesamtergebnis des PPP-Modells eine hohe Sensitivität gegenüber der Veränderung der Zeit aufweist, die ein Tigerweibchen braucht, um ihre Jungen aufzuziehen. Die Analyse zeigt auch, dass die Anzahl an abwandernden Tigern sensitiv gegenüber der individuellen Wahrnehmungsdistanz von Beute ist. Der Vergleich mit einem ähnlichen Räuber-Beute-Modell lässt vermuten, dass diese Wahrnehmungsdistanz eines Individuums generell als ein entscheidender Faktor für Räuber-Beute-Beziehungen in räumlich-expliziten Individuenmodellen an- gesehen werden kann. Die Parametrisierung der Individuellen Wahrnehmungsdistanz des Tigers wurde so gewahlt, dass die damit ermittelten Simulationsergebnisse den Beutekonsum des Tigers, wie in der Literatur beschrieben, weitgehen widerspiegeln. Sie ist somit für die weitere Anwendung im PPP-Modell ausreichend gut beschrieben.

Simulationsszenarien, welche verschiedene Habitatqualitäten sowie Landnutzungsmuster berücksichtigen, zeigen auch deren Bedeutung für die Mortalität und Migration der Beutetiere. Eine gute Habitatqualität hat eine geringe Mortalität der Beutetiere zur Folge, welche dann wiederum für den Tiger in ausreichender Zahl zur Verfügung stehen. Treten geringe Habitatqualitäten angrenzend an ein Habitat mit hoher Qualität auf, führte dies zu einer hohen Anzahl an abwandernden Beutetieren, womit sich die Ressourcen für den Tiger verringern. Die Landschaftsmerkmale sollten also bei der Vorhersage des Populationsfortbestandes des Sumatra-Tigers berücksichtigt werden. Die optimale Bewegung von zwei verschiedenen Beutetieren ergab eine hohe Beutedichte in einem Habitat mit hoher Qualität und stellte konzentriert Beute in einem Tigerhabitat bereit. Allerdings resultierte dies auch in einer geringeren Prädationsrate des Tigers, verglichen mit zufälligen oder artenspezifischen Bewegungen.

Das PPP-Modell wurde angewandt, um die Auswirkungen von Wilderei, Beutetierrückgang sowie die Kombination beider Faktoren auf die Aussterbewahrscheinlichkeit einer Tigerpopulation zu bewerten. Die Ergebnisse zeigen, dass die genannten Faktoren eine 100-prozentige Aussterbewahrscheinlichkeit innerhalb von 20 Jahren zur Folge haben, wenn die Dichte und Häufigkeit dieser Bedrohungen hoch sind. Die Dauer dieser Bedrohungen im System verursachte allerdings eine 100-prozentige Aussterbewahrscheinlichkeit nur für die Wilderei von Tigern. Betrachtet man unabhängig von Dichte und Häufigkeit einzig die Dauer der Bedrohung, führt lediglich die Wilderei zum 100%-igen Aussterben. Diese Ergebnisse können maßgeblich dazu beitragen, zukünftig Schutzprogramme gegen die Wilderei zu optimieren, um das Aussterben des Sumatra-Tigers zu verhindern.

Des Weiteren wurde der Einfluss von unterschiedlichen Landnutzungsmustern auf die Aussterbewahrscheinlichkeit und -zeit einer Sumatra-Tigerpopulation aufgezeigt. Die Integration von räumlichen GIS-Daten in das Modell ermöglichte einen Einblick in die Beziehungen zwischen Tiger, Beutetieren und Habitat. Die Ergebnisse zeigen, dass die Habitatqualität um Schutzgebiete herum eine wichtige Rolle für den Fortbestand der Population spielt. Die vorliegende Arbeit empfiehlt Agroforstsysteme als eine geeignete Landnutzungsform in der Nähe von Schutzgebieten, welche sowohl positive Effekte für den Tigerschutz bietet als auch mit den gegenwärtigen Landnutzungsmustern in Sumatra vereinbar erscheint.

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Contents

Chapter 1

Introduction

Summary: This chapter serves as the basic rationale of this study. The current decline in Sumatran Tiger population, habitat loss and the existing threat from humans are presented in Section 1.1 to provide insight into the problems facing the conservation of the Sumatran tiger. The current scientific findings in tiger ecology and conservation practices are elaborated on Section 1.2 to provide an insight into the challenges facing the Sumatran tiger conservation. The use of classical models and geo-infomation systems, particularly individual-based models for the development of conservation strategies are discussed in sections 1.3 and 1.4. Finally, research questions are outlined in Section 1.5 and the structure of the entire thesis is provided in Section 1.6.

1.1 Cornerstones of Sumatran Tiger Conservation

1.1.1 Population Status

Tiger conservation in Indonesia began as the result of a poignant story; the extinction of both the Javan tiger (*Panthera tigris sundaica*) and the Bali tiger (*Panthera tigris balica*) in the 20^{th} Century. The Sumatran tiger (*Panthera tigris sumatrae*) is the last sub-species of tigers in Indonesia which survives in the wild. Thus, Indonesian government classified this sub-species as protected species. This big cat on the Sumatra island is also categorized as a critically endangered species by the International Organization for Conservation of the Nature (IUCN, 2010). Additionally, the Convention on International Trade in Endangered Species of Wild Flora and Fauna designates this species in the first appendix, outlining that trading any part of this animal is strictly prohibited (CITES, 2010).

The population of the Sumatran tiger has been declining during the last two decades. Estimates of the population of this sub-species of tigers in the wild indicated a decrease in number, from 400 individuals in 1992 (Franklin et al., 1999) to 300 individuals, as indicated results by recent estimates in 2008 (Seidensticker et al., 2010). The major causal factors of the declines of the Sumatran tiger including prey depletion, tiger poaching and habitat destruction are explained as outlined in the following sections.

1.1.2 Sumatran Tiger and its Prey

As carnivores, tigers are dependent on prey availability. Prey density and size are two main factors that determine tiger populations in the wild. Tiger abundance, as a function of prey densities, were shown by the studies from Sunquist et al. (1999) and Karanth and M.Stith (1999). Those studies revealed that higher tiger densities were driven by higher prey densities. Tiger populations are not only affected by prey densities, but are also dependent on prey sizes (Biswas and Sankar, 2002). Tigers cannot survive and reproduce only with small-bodied prey, even if the density of such prey is high (Sunquist, 2010). The reduction of large-bodied prey population will cause a reduction in tiger population (Ramakrishnan et al., 1999). The tiger dependency on large-bodied prey is contrary to the fact that tigers are also flexible predators. Tigers are not only known to select large-bodied prey when resources are abundant (Karanth and Sunquist, 1995; Biswas and Sankar, 2002), but are also flexible with the ability to switch to smaller bodied prey, when prey density is low (Reddy et al., 2004).

The dependency of tigers on prey availability suggests that depletion of prey population is responsible for the decline in tiger populations (Ramakrishnan et al., 1999; Karanth et al., 2004). Prey depletion has been highlighted as a causal factor for tiger populations decline in many parts of the world such as in Laos PDR (Johnson et al., 2006), India (Karanth and Sunquist, 1995; Biswas and Sankar, 2002; Reddy et al., 2004), Nepal (Wegge et al., 2009), and Russia (Miquelle et al., 1999b). Improvements in prey density as a consequence of the establishment of a protected area, was followed by the recovery of tiger population (Wegge et al., 2009). Hence, one of the conservation strategy for tigers is to protect, maintain, and increase prey populations in several ways (Sunquist et al., 1999; Miquelle et al., 1999a; Seindensticker et al., 1999), such as expanding prey habitat by the establishment of a protected area or the resettlement of people from protected areas (Miquelle et al., 1999a; Wegge et al., 2009; Steinmetz et al., 2010).

The importance of prey population for tiger conservation is also evident for the Sumatran tiger. Studies have been done to detect the Sumatran tiger and its prey in different habitat types (Franklin et al., 1999; Linkie et al., 2003; O'Brien et al., 2003; Linkie et al., 2006; Hutajulu, 2007). However, among those studies, only the study by O'Brien et al. (2003) clearly states the relationship between prey and the Sumatran tiger densities. Furthermore, the lack of studies about the predation behaviour of the Sumatran tiger on large and small-bodied prey means that one of the basic foundations for Sumatran tiger conservation is overlooked.

The limited information on the relationship between the Sumatran tiger and its prey has been worsened by the evidence that this sub-species of tiger might be threatened by a mechanism/process behind prey depletion which has to be analyzed. The main causal factors are the massive habitat loss of prey (Kinnaird et al., 2003; Linkie et al., 2003, 2006; Gaveau et al., 2007) and the potential prey depletion effect resulting from poaching (Linkie et al., 2003; O'Brien et al., 2003; van Strien, 2006; Tilson and Nyhus, 2010). Numerous studies in the field ilustrate that poaching in tiger habitats is not only illegally removing tigers but also tiger prey species, including other endangered animal such as Rhinocheros (*Dicerorhinus sumatrensis*) (Linkie et al., 2003; O'Brien et al., 2003; van Strien, 2006; Tilson and Nyhus, 2010).

1.1.3 Poaching the Sumatran Tiger Population

The poaching of tigers has been highlighted as the main causal factor for the decline in tiger populations in the wild, and is driven by the conflict between humans and tigers (Tilson et al., 2010). This conflict resulted in the killing of tigers, a common phenomena in Indonesia and surrounding countries between 1600 to 1950 (Boomgaard, 2001). Nevertheless, the causal factors which determine poaching are varied, including human defence against tigers, cultural and political purposes, medicinal reasons, and commercial background (Boomgaard, 2001; Shepherd and Magnus, 2004; Nyhus and Tilson, 2004b; Tilson et al., 2010).

Several estimates about tiger poaching provide a proof that poaching has been threatening the Sumatran tiger population in the wild (Linkie et al., 2003; Shepherd and Magnus, 2004; O'Brien et al., 2003; Tilson et al., 2010). Demands on tiger parts are potentially high for Chinese medicines (Gratwicke et al., 2008) and may also be related to traditional beliefs (Tilson et al., 2010). A recent study on the poaching estimates that tiger poaching over the past 20 years may have been higher than previously estimated; previous estimates approximated that 51 tigers/year (Shepherd and Magnus, 2004) were poached, while current estimates are as high as 56 tigers/year within 6 province in Sumatra (Tilson et al., 2010). In spite of the high rate of international demand for tiger body parts, which was considered for an earlier study completed by Shepherd and Magnus (2004), local demands also play important roles for the increase in poaching rates on Sumatra island (Tilson et al., 2010). This evidence ilustrated that poaching is not only driven by international markets but also local demands, an alarming situation for the Sumatran tiger population.

Surprisingly, the recent findings about the rate of poaching showed that the number of tigers poached in core areas of national parks represented 58% of the total tigers poached, a higher percentage than other protected area categories such as protected forests or wildlife reserves (Tilson et al., 2010). The findings highlighted that protected areas potentially reduce the conflict. If a single protected area surrounded by unfriendly landuse, it is not secure enough to protect tiger population in the wild from poaching.

In addition, human-tiger conflict is controversial and a product of socio-economic and political landscapes, which are concerned with economic value of protected animals (Graham et al., 2005). Tiger poaching is mainly caused by conflict over space between humans and tigers, a relationship that is categorized by Nyhus and Tilson (2004b) into three different types. First is when tigers and people overlap in a relatively small area, such as the edge of the forest or protected areas. There is a low probability of conflict. Second is when people have access to forests, there is a high-level of tiger food resources, the probability of conflict is high. Finally, when settlements are established within tiger habitats, there is a high probability of conflict during the initial establishment of the settlements which may be lowered due to the reduction of tiger populations as a result of earlier conflict. Consequently, human-tiger conflicts should be less common in protected areas and more common in intermediate disturbance areas where tigers and people coexist (Nyhus and Tilson, 2004b).

1.1.4 Massive Habitat Modification in Sumatran Island

Tigers are able to persist in a very wide range of habitat conditions. Tigers are distributed across different habitat conditions, such as hot-dry forest in Rajashtan, tidal mangrove swamps in SundarBarns, tropical forest rain forest in Sumatra, and temperate and boreal forest of Russian Far East (Miquelle et al., 1999a; Sunquist, 2010). However, tigers are also known to have site fidelity and to be territorial in order to successfully survive and reproduce (Miquelle et al., 1999a).

The amount of habitat available for tiger in India, Indo-China, and South-

Figure 1.1: Map of predicted deforestation on Sumatra island during 1990-2000 (Gaveau et al., 2009). Colours represent types of coverage: remaining forest coverage (green), deforested areas (red), mangrove (pink), and logging road (yellow).

east Asia diminished by approximately 15-20% between 1995-2005 (Dinerstein et al., 2006). Similarly, the tropical forests in Sumatra island has been on the receiving end of severe consequences from development during the last two decades. Figure 1.1 ilustrates the predicted forest dissapearance in Sumatra, at a rate of 2.56% per year between 1990-2000 (Gaveau et al., 2009). More severe conditions were evident in central of Sumatra; forest cover in the Riau province dramatically reduced when 60% of the forest cover in this province dissapeared from 1982 to 2007 (Uryu et al., 2007).

Habitat loss in the natural tropical forest is mainly caused by deforestation through logging activities (Gaveau et al., 2007; Linkie et al., 2003) and the conversion of forest into other land-use types. Forest conversion is a result of activities such as settlement establishment, agricultural encroachment, and palm-oil plantation development (Kinnaird et al., 2003; Uryu et al., 2007; Maddox et al., 2007; Gaveau et al., 2007). However, these activities not only occur outside, but also within the protected areas. Recent findings on the protected areas evaluation in South-East Asia showed that protected areas are less effective for protecting forests as the ratio of forest loss within protected areas was larger than outside these reserves (Gaveau et al., 2007, 2009). On a smaller scale, at the level of individual protected area, several studies showed that deforestation also occurred within national parks. The deforestation within the Bukit Barisan National Park between 1985-1999 was estimated to be at the rate of 2% per year, and predicting that the park will be dominated by agricultural area in 2010 (Kinnaird et al., 2003). Another example from Kerinci Seblat National Park showed that the rate of deforestation within the park increased 1.1 % per year between 1985 to 1992. These examples highlight that protected areas are not yet self-protected against deforestation.

The nature of tigers to establish homerange/territory for surviving and reproducing has promoted the idea to establish enough space for tiger populations. The basic need of space for tigers has led conservationists to focus their attentions on maintaining or even expanding habitat availability for large mammals in general (Nyhus and Tilson, 2004a). Additionally, mainstreaming the idea of securing habitat for tigers and other mammals in national and regional development plans was endorsed for ensuring the survival of the tiger in the landscape (Dinerstein et al., 2006). Hence, integration of conservation areas within existing land-use plans have emerged from the idea of reducing potential human-tiger conflict and addressing the challenges associated with human population growth near protected areas for tigers (Linkie and Christie, 2007).

1.1.5 Protected Areas Networks

Political situations in Indonesia has apparently created a complex situation for the management of protected areas for Sumatran tiger populations. Both local and central government have established different types of protected areas which are managed at different governmental levels. The ministry of Forestry for the Republic of Indonesia established six types of protected areas, all of which under the management of the central government, including: strict nature reserve, national park, wildlife sanctuary, nature recreational park, game hunting park, and grand forest park. The total size of these protected areas account for 4,873,482 ha on Sumatra island (Kehutanan, 2009). Sumatra's local government, provincial and district levels, also manages protected forests with a total size of 5,814,093 ha. In total, Sumatran protected areas, under management of both the local and central government, covers 10,687,575 ha, 40% of the total forest coverage in this island.

Figure 1.2 ilustrates the proportion of nature conservation areas under the control of central government, protected forests under local government management, and non-protected forests in each province of Sumatra. Most provinces in Sumatra a greater proportion of non-protected forests, with the exception of Aceh, West Sumatra, Bengkulu, and Lampung. The fact that protected areas are not yet well protected and are less effective for reducing deforestation in Sumatra (Linkie et al., 2004; Gaveau et al., 2007), hightlights that relying only on the existing protected areas will not be enough for the conservation of Sumatran tiger.

1.2 Scientific Challenges to Tiger Conservation

1.2.1 Prey Depletion and Tiger Poaching Paradigms

The inclusion of tiger poaching and prey depletion as important factors for the survival of tigers have led to two different paradigms; the prey depletion and the tiger poaching paradigms. The prey depletion paradigm determines prey populations as a critical factor for tiger population in the wild. Therefore, one priority for tiger conservation is to recover prey populations by habitat improvement. The tiger poaching paradigm emphasizes the importance of poaching on tiger mortality in the wild as poaching has been highlighted as one of major causal factors of declining tiger population in the wild (O'Brien et al., 2003). Poaching explained the recent rapid decline in tiger populations as a results of increasing demand for products created from tiger parts (Dinerstein et al., 2007; Shepherd and Magnus, 2004). Therefore, reducing numbers of poachers by surveillance is then an important approach for tiger conservation (Linkie et al., 2003; Kenney et al., 1995).

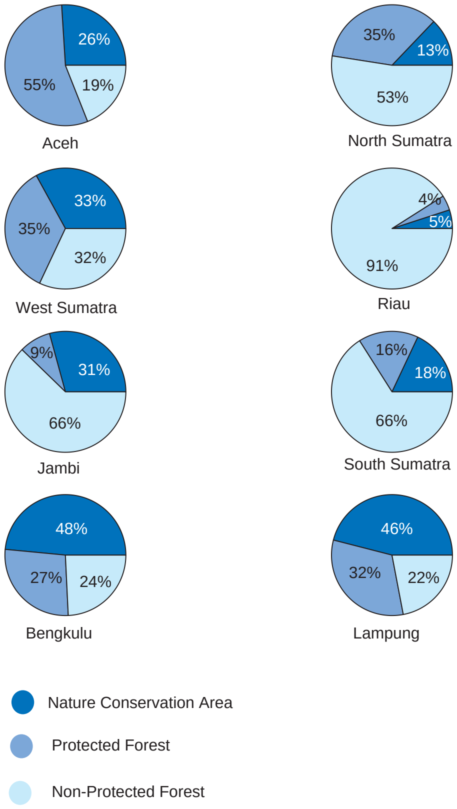


Figure 1.2: The proportion of nature conservation areas under the central government management(NC), protected forest (PF) and non-protected forest (NPA) in each province of Sumatra. Source: Kehutanan (2009)

Modeling (Karanth and M.Stith, 1999; Kenney et al., 1995; Chapron et al., 2008) and empirical studies have been carried out to support both the tiger poaching and prey depletion premises (Miquelle et al., 1999a; Ramakrishnan et al., 1999; Karanth et al., 2004, 2006; Linkie et al., 2003). However, poaching in tiger habitats is not only aimed at illegally hunting tigers, but also its prey (Linkie et al., 2003; Steinmetz et al., 2010; van Strien, 2006). It seems that none of the studies evaluated the impact of the simultaneous threats on tiger and prey, which might increase the risk of tiger extinction. An effective conservation measure should understand the magnitude of significant factors on population persistence (Fahrig, 2001). Therefore, insight into impact of the combination of prey depletion and tiger poaching is important for the science of tiger conservation.

The evidence of population recovery of Amur tiger (Galster and Eliot, 1999) and prey population (Steinmetz et al., 2010) after the deployment of anti-poaching programs have motivated similar program for the Sumatran tiger (van Strien, 2006; Linkie et al., 2003). The aims of these programs are to reduce poaching of both tigers and prey species. Results from Galster and Eliot (1999) have shown that tigers are able to recover their population after the removal of poaching. Similar programs are also being deployed in Sumatran tiger habitats and have successfully disarmed poaching of both tiger and its prey (van Strien, 2006; Linkie et al., 2003). However, these programs did not attempt to measure possible population extinction after poaching removal. Since many Sumatran tiger populations are small and fragmented, population recovery after anti-poaching programs might not be achieved due to environmental and demographic stochasticity. The understanding of potential extinction after severe tiger and prey poaching pressure in combination with an anti-poaching program will enhance our ability to develop a sound conservation program for the Sumatran tiger.

1.2.2 Tigers in Heterogeneous Landscape

As a large carnivore, the Sumatran tiger requires large protected areas to provide enough food and space for reproduction. The social, political and economic realities of many landscapes in Asia have turned large suitable habitats into small, fragmented ones (Nyhus and Tilson, 2004b). This coupled with the difficulty of halting forest loss has worsened the situation (Kinnaird et al., 2003). Habitat loss and destruction is an increasing serious problem for many protected areas on Sumatra island (O'Brien et al., 2003; Linkie et al., 2004; Gaveau et al., 2007, 2009). Deforestation creates larger border zones than an intact habitat. This edge is a new habitat type for tigers, one which tigers may not have previously experienced. Conflict with people on reserve borders is the major cause of mortality in such populations, so much so that border areas represent population sinks (Woodroffe and Ginsberg, 1998; O'Brien et al., 2003). Therefore the conservation effort should not only provide attention to the provision of large enough habitats, but must also deal with human-wildlife conflict when new land uses emerge in the surroundings. Thus, the need for integrated and comprehensive management strategies that take into account the complexity of landscapes surrounding protected areas has become more urgent in recent decades.

In order to integrate the surrounding landscape with protected areas, particular attention should be paid to the landscape structure as landscape structures play an important role in population dynamics (Fahrig, 2007b). Sumatran tiger populations have been facing habitat fragmentation and possible population isolation, due to forest conversion, over the course of the last three decades (Franklin et al., 1999; Linkie et al., 2006; Gaveau et al., 2007). The landscape of Sumatra is comprised of many land-use types, such as logging concessions, agriculture, settlements, oil-palm plantations, as well as mining operations. Although a significant effort has been conducted for Sumatran tiger conservation, very little progress has been achieved for the tiger conservation in Sumatra (Tilson and Nyhus, 2010). A challenge for conserving the Sumatran tiger is to understand how tigers respond to those land-uses and which landscape configurations are able to support tiger populations. Since individual variation and behaviour is important and affect the dynamics of the population (Revilla and Wiegand, 2008), the response of the Sumatran tiger to different habitat types should be understood at an individual level.

Several studies ilustrate the distribution patterns of the Sumatran tiger and its prey in different habitat types, such as tropical forest within protected areas (Franklin et al., 1999; Kinnaird et al., 2003; Linkie et al., 2003;

O'Brien et al., 2003), agroforestry (Nyhus and Tilson, 2004b), palm oil plantations (Maddox et al., 2007) and logging concessions (Linkie et al., 2008). These patterns of population distribution in different levels and types of human altered landscape is an important achievement for Sumatran tiger conservation. However, insight into the behavioural studies about how tigers respond to different land-use types in the landscape levels is still insufficient. This knowledge will enhance our undertanding and is important for conservation strategy development at the landscape level. Furthermore, the cryptic characteristics of the tiger and the complexity of the existing landscape configuration have resulted in very few behavioural studies on this sub-species of tigers, presenting us with further limitations for understanding their response to landscape configuration.

Considering the rapid loss of tropical forests on the Island of Sumatra, the emergence of various habitat types surrounding protected areas and the lack of knowledge about the response of tigers and prey to various habitat types, the conservation of this tiger requires an alternative approach which is able to understand behavioural responses of tigers at individual levels and the consequences at population or landscape levels.

1.3 Roles of Modelling in Tiger Conservation

Understanding the relative effect of factors that determine population persistence is an important step for the conservation of endangered species, as suggested by Fahrig (2001). Modelling has been used for tiger conservation in three main ways, including: to gain insights into the effect of a particular factor for the tiger population dynamics, to predict the probability of extinction from the effect of management choice or disturbance, and to develop conservation strategies.

The use of modelling to understand the effect of particular factors were demonstrated by several studies, such as comparing the effect of tiger poaching and prey depletion. Kenney et al. (1995) tested the effect of poaching on the long-term population persistence of tigers, which came to be known as the tiger poaching paradigm identified above. This study was contested by Karanth and M.Stith (1999) and their model of the prey depletion paradigm. A recent modelling study by Chapron et al. (2008) has supported the importance of tiger loss from poaching and the possible extinction of tiger populations. The TIGMOD model, an individual-based model, successfully simulated the conflict between tiger and humans in Nepal Ahearn et al. (2001).

A common approach for endangered animal conservation is the use of the Population Viability Analysis (PVA). PVAs play important roles for the conservation of endangered species (Boyce, 1992). The first PVA for Sumatran tiger was conducted in 1992, in order to assess population and habitat for tigers (Franklin et al., 1999). PVA, in terms of assessing the viability of small/local population, have been recently been used for several national parks/localities in Sumatra. Linkie et al. (2006) assessed the viability of the tiger population in the Kerinci Seblat National Park based on a spatially explicit habitat model using geographical information systems (GIS). Current studies by Uryu et al. (2007) has provided a snapshot of the forest disappearance and the use of geographic information systems (GIS) for population viability analysis of the Sumatran tiger population in Central Sumatra. However, the use of GIS will be more meaningful if connected with mechanistic theories for predicting population dynamics as a function of landscape attributes (Kareiva and Wennergren, 1995).

One important product of PVAs is the prediction of the time to extinction for an endangered species. There exists two common measures: arithmetic mean time and intrinsic mean time to extinction. Arithmetic time to extinction was criticized by Boyce (1992) and Grimm and Wissel (2004) because this measure might mislead the prediction due to the fact that the distribution of time to extinction is skewed. In addition, no concensus on quantification of persistence and the viability of population in PVA models has generated the concept of the intrinsic time to extinction (Grimm and Wissel, 2004). Intrinsic mean time to extinction was introduced by Grimm and Wissel (2004) to the arithmetic time to extinction by providing measure which shows intrinsic ability of a population to survive and reducing the effect of initialization. This measure also reduce the effect of skewed data distribution. Therefore, any PVA for tigers should use this measurement for better assessment about the probability of extinction.

The use of modelling for the development of global conservation strategis were demonstrated by Wikramanayake et al. (1998) and Dinerstein et al. (2006). The need of integrating landscapes surrounding protected areas has been translated into the establishment of the Tiger Conservation Unit (TCU) and Tiger Conservation Landscape (TCL). TCU provided basic knowledge for setting priorities for the conservation of tigers in nature throughout all geographical ranges of tigers. The TCU was defined by tiger habitat assessment for their integrity, poaching pressures, and trends in tiger population with the ultimate goal of the conservation of "tigerness" (Wikramanayake et al., 1998; Sanderson et al., 2010). The assessments were carried out by obtaining expert oppinion about the future of tiger populations at given habitat types (Wikramanayake et al., 1998). This approach, which highly relied on expert oppinions and inadequate database design (Dinerstein et al., 2006) led to encourage the development of Tiger Conservation Landscape (TCL). The main revision from the previous approach is the establishment of a set of rules to define priorities which were based on tiger observations in the wild, tiger distribution in various land cover, human influence index, minimum patch size required for a tiger population, and the rule of connectivity (Dinerstein et al., 2006; Sanderson et al., 2010).

The TCLs were assessed by three primary data sets, including the most recent land cover data, new tiger data, and human influence data. The categories are practical for setting priorities for tiger conservation across landscapes. However, at the same time, the framework also has been limited by the quality of the data being used, such as the availability of land-cover maps, limited studies about the tiger-prey relationship, and the lack of understanding about tiger dispersal behaviour (Dinerstein et al., 2006). Additionanlly, the strategy aims to cover the global biogeographical range of tiger and was not supported by local conditions such as land-use types that surround priority areas at study sites. Since the persistence of a population should consider the landscape configuration (Lindenmayer et al., 2008; Haines et al., 2005; Hanski, 1998), the use of modelling for tiger conservation should incorporate the surrounding landuse of certain protected/priority areas.

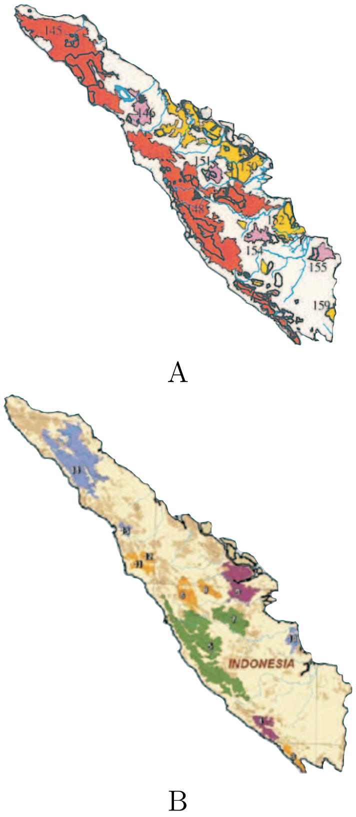


Figure 1.3: Two maps of landscape-based conservation strategies on Sumatra island for tigers. (A) is the Tiger Conservation Unit (TCU) map (Wikramanayake et al., 1998). (B) is the map of Tiger Conservation Landscape (Dinerstein et al., 2006). TCL is an improved version from TCU which consider recent land cover data, tiger distribution and human influence data. Source of Maps: Wikramanayake et al. (1998) and Dinerstein et al. (2006).

Modelling is one potential approach for the Sumatran tiger conservation. However, the existing modelling approaches are mainly based on expert opinions and less meaningful for the conservation purpose due to a lack of understanding about the response of tiger and their prey populations to the landscape configuration. The challenge of science on the Sumatran tiger conservation is to develop a model which incorporates all important factors associated with the population response of the tiger to changes in habitat, the presence of humans as well as prey dynamics.

1.4 Individual-Based Models for Tiger Conservation

The basic principle of the Individual-based model(IBM) is that a population or a system consists of discrete individuals which have a set of traits and can be distinguished from other individuals (DeAngelis and Mooij, 2005; Grimm and Railsback, 2005). This means that IBMs are able to include individual variation in much more detail than previous modelling approaches such as classical differential equations, and simulates the interaction between individuals and their environment (DeAngelis and Mooij, 2005). IBMs have the ability to simulate the behaviour of individuals and predict interactions depending on complex environmental conditions (Ahearn et al., 2001; Grimm and Railsback, 2005). The emergence of the model such as population dynamics and spatial arrangement can be observed as results of interaction between individuals and their environment. IBM also provides tools to evaluate different environmental and management scenarios using all available knowledge independently, whether they are quantitative or qualitative in nature. This approach has been proven to be suitable for evaluating the impact of a variety of land-use policy instruments and predicting long-term response to changes in management practices (Grimm and Railsback, 2005). The use of IBM would therefore appear to be a promising option that would complement existing tiger conservation programs. For these reasons, IBM was chosen for this study as a tool for understanding the response of tiger populations to the different landscape configurations.

IBM was first used in tiger conservation science to evaluate the effect of poaching on tiger populations by Kenney et al. (1995). The first IBM for tigers was spatially explicit but assumed that prey and landscape configuration were not the determinating factors for the survival of tigers. The second IBM was the TIGMOD model (Ahearn et al., 2001), which aimed to evaluate the effect of human-tiger conflict in Nepal on the tiger population. The TIGMOD included almost all of the most important individual tiger behaviour and was simulated in one-year time horizon. The TIGMOD simulated interaction between tiger and prey in a spatially explicit way. However, understanding the response of the predator population from landscape configuration should involve the three-trophic relationship of habitat-prey-predator (Ryall and Fahrig, 2006; Baeza and Estades, 2010). Additionally, the intervening landscape affects the population dynamics, thus any model used for population persistence should integrate landscape configuration (Russell et al., 2003). The existing IBMs for tigers have not yet demonstrated the indirect relationship between tiger and its habitat with consideration for the surrounding landscape.

1.5 Research Questions

The objective of the present study is to investigate the potential effect of direct human influence and landscape configuration for sustaining the Sumatran tiger population in central Sumatra. This should include sufficient understanding at the landscape level as well as at the individual level. This study demonstrates the development of the Panthera Population Persistence (PPP), an individual-based model for the conservation of the Sumatran tiger population. The model includes all important traits which are necessary to distinguish individuals, and recognizes individual behaviour in much more details than existing models, simulates major important behaviours of tigers response to other individuals and different environmental condition, and parameterizes the model for the application in the Central Sumatran landscape. The purpose of this study is to provide recommendations for the conservation of the Sumatran tiger population.

To address this main objective, the following questions will be covered:

1. How does the relative importance of tiger poaching, prey depletion, and a combination of these factors affect the Sumatran tiger's probability of extinction?
2. Is the anti-poaching program able to reduce the extinction probability of the Sumatran tiger population following poaching pressures?
3. Do existing landscape configurations support conservation of the Sumatran tiger?
4. What is the best landscape configuration for sustaining tigers population in Central Sumatra ?

1.6 Thesis Structures

The following Chapter (2) serves as a summary of theories for understanding and interpreting the results of this study. Chapter 3 provides a description of the study areas and the development of the land-use map, the description of the basic Panthera Population Persistence (PPP) model, and the model analyses being used for this study. Chapter 4 is divided into four main sections. The section 4.1 demonstrates the use of sensitivity analysis to gain insight into the predator-prey relationship by comparing the PPP model with a model which has similar predation processes. Section 4.2 demonstrates the estimation and justification of the hunting-radius parameter through known tiger-prey relationship and the use of the PPP model to test the effect of habitat qualities, landscape configuration and the movement decisions made by prey on the prey's mortality and migration. Section 4.3 ilustrates the application of the PPP model to answer the first research question about the relative importance of poaching, prey depletion, and their combination, for the extinction probability of the Sumatran tiger population in Central Sumatra. This section also address the second research question which focusses on the roles of anti-poaching programs for the survival of the Sumatran tiger population after recieving pressure from poaching. Section 4.4 demonstrates the use of the PPP model to understand the behaviour response mechanisms of tigers to the presence of various landscape configurations and to suggest the best landscape configuration for the survival of the Sumatran tiger population. Chapter 5 summaries the findings in previous chapter, bringing into discussion with previous literature and findings. Chapter 6 serves as conclusion and offers recomendations for future research and the conservation of the Sumatran tiger.

Chapter 2

Literature Review

Summary: The previous chapter described the state-of-the-art presented by tiger conservation and how this study formulated the research questions to address those chalanges. This chapter serves as a summary of the theoretical foundations which are necessary for the development of an individual-based model for the Sumatran tiger conservation, as well as for interpreting the results of this study.

2.1 Fragmentation and Population Dynamics

2.1.1 Habitat/Landscape Fragmentation

Habitat fragmentation is usually defined as "*a landscape-scale process involving both habitat loss and the breaking apart of habitat*" (Fahrig, 2003). Fragmentation, as a process, starts from a large continuous habitat, which is then subdivided into smaller and isolated habitat patches. Fragmentation implies into six habitat patterns, in this example: (a) decreasing size of habitat; (b) greater number of habitat patches; (c) reduced size of habitat-patches; (d) increasing isolation of habitat patches; (e) edge creation; and (f) increasing variation in habitat qualities and landscape configurations (Fahrig, 2003; Woodroffe and Ginsberg, 1998; Moilanen and Hanski, 1998; Wiegand et al., 1999). Figure 2.1 illustrates the fragmentation process and its results on different landscape configurations.

Once fragmentation occurs in the landscape, a population experiences population reduction and may become a smaller population (Lande, 1987). Habitat amount and quality play important roles in the variation in population size (Wiegand et al., 2005). When a landscape contains many habitat patches, it will have more edges per given habitat amount. The probability of individuals to leave habitat patches and remain within the matrix is higher than in non-fragmented landscapes. This may increase mortality rates and reduce a population's reproductive rate.

Habitat fragmentation also potentially affects the population persistence of a population, thus increasing the extinction threshold (Fahrig, 2002). The most important effect of habitat fragmentation for a population is isolation. When a large population is fragmented into several smaller isolated sub-populations, the dynamics of the population is disrupted and dispersal patterns are reduced (Mech and Hallet, 2001; Coulon et al., 2004; Dixon et al., 2007). The major consequences of isolation concerns population genetics. Genetic variations within and among populations are a prerequisite for the survival and adaptability of a population. Isolation is expected to decrease both heterozygosity and the number of alleles in a population through genetic drift (Hartl et al., 2003). In addition, the absence of gene flow, as a result of isolation among sub-populations, affects depletion in

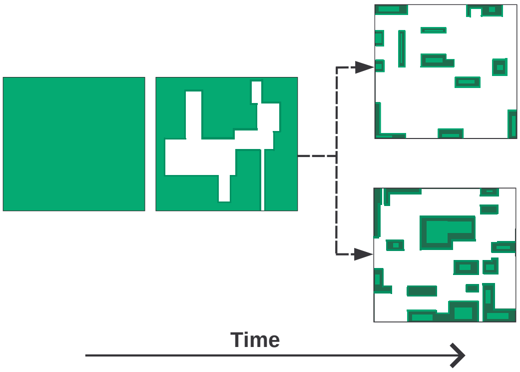


Figure 2.1: Conceptual illustration of the process of fragmentation at the landscape level which affects the total amount of habitat, number of habitat patches and size, isolation, edge effect, and habitat quality (Fahrig, 2003; Woodroffe and Ginsberg, 1998; Moilanen and Hanski, 1998). The dashed arrows denotes that the end result of fragmentation can present different landscape configurations.

genetic variations which can lead to population extinction in the future (Hartl et al., 2003; Dixon et al., 2007).

2.1.2 Effect of Fragmentation and Habitat Loss on Predator-Prey Populations

To understand the effect of habitat change/modification on predator-prey populations, four important factors should be considered including: the feeding habits of the predator; the relationship between habitat-prey-predator; the amount of habitat loss; the migration of prey from predator-prey habitat; and the effect of matrix on the predator population (Ryall and Fahrig, 2006).

The feeding habits of a predator, whether it is specialist, generalist, or omnivore, is a fundamental in a predator's prey selection. A specialist is restricted to one focal prey, whereas a generalist or an omnivore have multiple prey options. The relationship between predator and prey in term of habitat, can also be used to determine feeding habits. A specialist is restricted to the same habitat type as its main prey. An omnivore can use several habitat types, but has higher survival rate in the prey habitat. Whereas a generalist predator lives primarily outside of the focal preys habitat (Ryall and Fahrig, 2006).

Trophic position has a major role in determining the effect of habitat loss/destruction on certain species. For a predator, habitat destruction may lead to a destructive process, whereas a prey population may benefit from the release of a predator but would also be negatively affected due to habitat reduction (Bascompte and Sole, 1998). The strongest negative effect of the loss of prey habitat is evidenced by specialist predators, followed by omnivores and generalists (Ryall and Fahrig, 2006). When the feeding and habitat of a predator is restricted to the same habitat type as the main prey (specialist predator), the effect of habitat loss to its population is much stronger than that experienced by a prey population (Figure 2.2a). An omnivore is able to use various habitat types but it has a high dependency on the major prey's habitat. This predator type is able to switch to other prey but has a high mortality rate when habitat of the major prey is lost (Figure 2.2b). A generalist predator primarily lives within the prey matrix, the extinction of this type of predator occurs when habitat loss occurs on a large scale (Ryall and Fahrig, 2006; Bascompte and Sole, 1998).

Border area or edge has particular effect on predator populations. The effect of border area on predator populations is not only due to altered interaction between predator and prey, but also due to conflict between humans and predators. Human induced mortality contributes more to the extinction of populations of large carnivores isolated on small reserves than do stochastic processes (Woodroffe and Ginsberg, 1998).

2.2 Population Extinction and its measures

2.2.1 Causal Factors for Population Extinction

A global analysis on the extinction risk of mammals revealed that among known mammals species, 25% of them are facing an extinction risk, and at least 11% of total terrestrial habitat on earth should be managed for

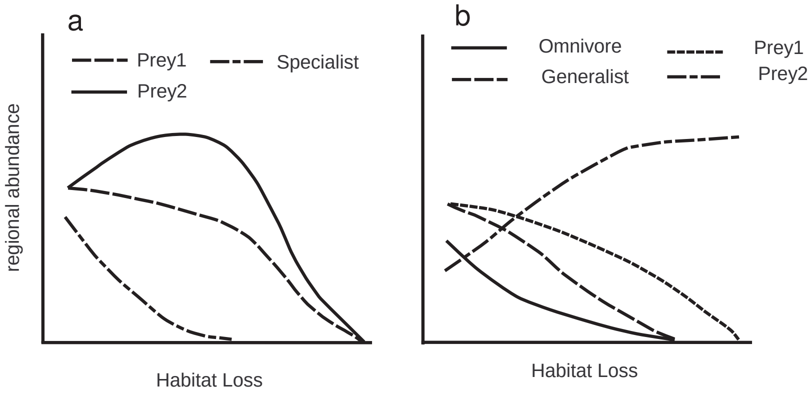


Figure 2.2: Conceptual diagram of the predicted effect of habitat loss on predator-prey populations, including: (a) Population dynamics of a specialist predator and two prey species; and (b) population dynamics of omnivore and generalist predators and two prey species. Prey 1 corresponds to omnivore in (b) and prey 2 is the main prey for the generalist predator.(Redrawn from Ryall and Fahrig (2006))

conservation (Ceballos et al., 2005). The extinction risks for mammals are driven by multiple causes that are a combination of both intrinsic and external factors. Intrinsic factors can be represented by body size, population density, genetic variation, etc. Particularly, genetic variations within and among a population is a prerequisite for the survival and adaptability of populations (Hartl et al., 2003).

Environmental factors such as the size and location of the geographical range and the levels of human impact propel the extinction risk of smaller mammals, whereas larger species are driven by the combination between intrinsic properties and environmental factors (Cardillo et al., 2005). Studies on the phylogenies of carnivores and primates revealed that high trophic levels, low population density, and limited geographical range are major factors in the risk of extinction (Purvis et al., 2000). Additionally, the indirect relationship between the extinction of a species and habitat destruction have suggested that environmental factors play important roles in the persistence of a population (Nakagiri et al., 2001). For example, road development affects the persistence of an animal population through habitat loss, fragmentation, traffic mortality, and inaccessible habitats (Jaeger et al., 2005).

Extinction might occur in a population when mortality and emigration rates are higher than birth and immigration rate, which reduces the population number to zero (Mace et al., 2008). Population extinction can also happen in small populations. A small population is highly affected by demographic stochasticity, where random variations in birth and death rates may lead to extinction (Mace et al., 2008). In a closed and small population, inbreeding is almost unavoidable due to the fact that all individuals become related to each other (Ralls et al., 2001). For large populations, extinction is mainly caused by external factors (Coughley, 1994).

The scale of population extinction is divided into two main scales; local population and meta-population. The cause of local extinction is stochasticity in demographic, environment, genetic, and extrinsic causes due to habitat loss and persecution by humans. The metapopulation extinction is mainly due to metapopulation processes; stochastic process of migration from small population and extinction-colonization process. The metapopulation extinction also can be affected by extrinsic causes such as specific enemies, habitat loss, and fragmentation lead to eventual extinction (Hanski, 2005).

Population size alone is not a good predictor for estimating extinction risks for large carnivores in protected areas. Extinction of large carnivore can be derived from two factors; both the presence of an edge effect and conflict with human are the major causes of mortality which lead to population extinction (Woodroffe and Ginsberg, 1998). Edge effect and isolation are also known to have a profound effect on the extinction of mammals in smaller reserve sizes. In particular, processes outside protected areas have an unexpected strong effect on the species within the reserves (Parks and Harcourt, 2002). Furthermore, the landscape contex surrounding a protected area has a strong effect on the density and persistence of predator-prey systems (Baeza and Estades, 2010). Thus, landscape configuration should be considered for projecting population persistence for a given species (Russell et al., 2003).

2.2.2 Extinction Measures

To develop conservation priorities, the International Union for Conservation of the Nature (IUCN) categorizes a species into two types of extinction: extinct and extinct in the wild. Both extinct and extinct in the wild represent the last time a species was observed in the wild (Mace et al., 2008). For conservation measures using modelling approaches, extinction can be represented by absolute extinction or quasi-extinction (Grimm and Wissel, 2004). Absolute extinction is when the population reaches 0 (zero) and no individuals persists. Quasi-extinction indicates that a population is going to become extinct but the population density does not necesarily reach zero, for example only one of sex classes remains or only very old individuals, which are incapable to reproduce, remain. Extinction of a population can be measured using several approaches, as described below.

Probability of Extinction

Probability of extinction is denoted as $\mathrm{P}_0(t)$, the probability of a population to extinct at t time. $\mathrm{P}_0(t)$ is the most common measure for extinction models. The calculation involves a simple proportion between the number of simulations resulting population extinction with the total number of simulations.

Extinction and Survial Threshold

The extinction threshold ($P_E thresh$)is commonly used to assess the minimum proportion, or size, or amount of habitats which are required for certain population to persist in the landscape (Fahrig, 2002; Lande, 1987). This value represents the effect of habitat parameters on the persistence of a certain population. The extintion threshold occurs when both the mortality and reproduction rate are in balance due to the amount of habitat. When the amount of habitat decreases, such as from habitat loss, the mortality rate will increase. Thus, a certain habitat amount where reproduction rate could outweigh the mortality rate, defines the extinction threshold. Therefore, any factor such as fragmentation which affects the amount of available habitat also affects the balance (Fahrig, 2002). The extinction threshold is sensitive to reproduction rates; and improvements in matrix quality can have a substantial effect on the extinction threshold (Fahrig, 2001, 2002).

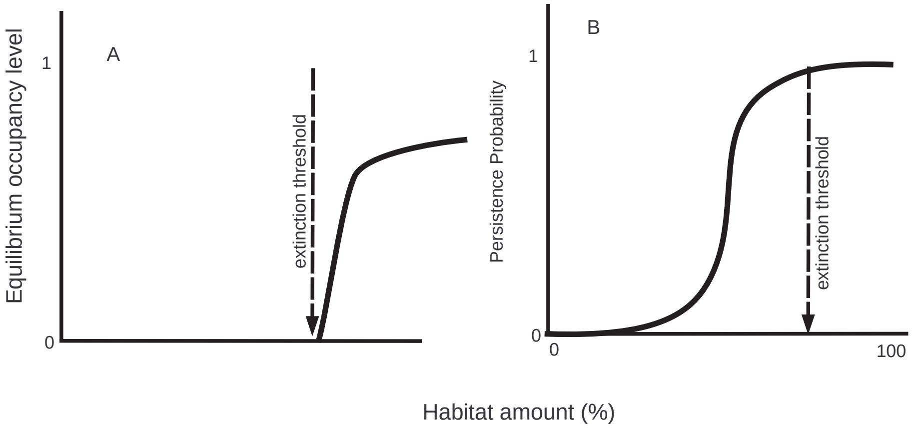


Figure 2.3: Illustration of two extinction threshold concepts. (A) represents the threshold where the proportion of the landscape occupied is 0. (B) is the threshold where the probability of long-term survival is below 1, indicating a minimum amount of habitat(Redrawn from Fahrig (2002)). For the practical application, the concrete value of $P_E thresh$ ranges between 0.95 and 0.99 (Hildebrandt et al., 2006).

Two approaches have been used to define the extinction threshold (Fahrig, 2002). The first is to define the amount of habitat necessarily to sustain a population. This approach is represented by the proportion of the landscape that is occupied by the population (Fig. 2.3A). The second approach is to depict the probability of long-term population survival, represents the minimum amount of habitat for a population (Fig. 2.3B). Sometimes, the $P_E thresh$ is defined as a value $\mathrm{P}_0(t)$ between 5% and 1% (Hildebrandt et al., 2006).

Despite the importance of the extinction threshold for predicting population survival, this measure is mainly based on the effort to avoid extinction of a population at the lowest probability. However, since humans developments have affected many large-bodied predators, forcing them to face extinction, the probability of extinction for these animals is higher than other types of animals (Cardillo et al., 2005). The use of extinction threshold might be meaningless due to this higher probability of extinction, as a result of both intrinsic and extrinsic factors as presented in Sub-section 2.2.1.

In addition, the application of the extinction threshold for evaluating the effect of habitat amounts for a certain population (Fahrig, 2002; Lande, 1987; Grimm and Storch, 2000) creates the impression that this measure can only be used for evaluating the effect of habitat amounts on population persistence and therefore not appropiate for other factors such as human conflict or edge effect, and landscape configurations. These factors have been recognized as important factors for large-bodied predators inhabitating a small reserve and surrounded by different land-use types (Woodroffe and Ginsberg, 1998; Parks and Harcourt, 2002; Russell et al., 2003).

Large-bodied predator populations face many threats from humans development. Thus, a threshold will be more meaningful for conservation if it identifies not only the acceptable habitat size being disturbed, but also includes many determining factors, while identifying what characteristics enable a population to avoid a 100% probability extinction. In the conservation of highly threatened species like tigers, investigating whether the population still has the probability to survive and define suggested conservation actions that would reduce the extinction probability may provide a realistic solution.

This study introduces a threshold where survival might occur; the "*survival threshold*" ($P_S thresh$) is a reverse point of view from the extinction threshold under different conditions. The definition of the survival threshold has been used for evaluating predator-prey system under the effect of polution (Huaping and Zhien, 1991). Instead of defining the threshold as the lowest probability of a population's ability to survive, the definition was similar to the extinction threshold as described by Fahrig (2002). Additionally, the use of the survival threshold in their model did not reflect how the model could be used for highly endangered species such as tigers. Thus, a new definition of the survival threshold will be meaningful for the conservation of the Sumatran tiger and other large-bodied predators in general. The practical measure of the $P_S thresh$ is defined by the value of $P_0 t$ between 95% and 99% as shown in Figure 2.4.

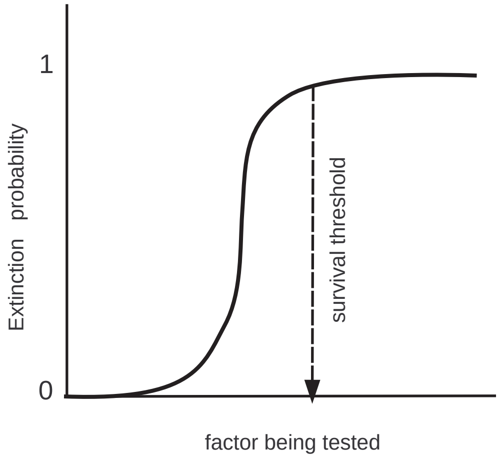


Figure 2.4: Conceptual diagram of the survival threshold of a population where the threshold is defined by the probability of extinction, $P_S thresh < 1$. Similar to $P_E thresh$ (Fig. 2.3A), one would define the $P_S thresh$ value between 0.95 and 0.99 in practical applications.

Time to Extinction

" When will a population experience extinction in the future ?". This is one of the most fundamental questions in the conservation of an endangered species that faces multiple threats to its population persistence. For conservation purposes, the intrinsic mean time to extinction (Tm) is very important to provide a careful prediction. Unlike the arithmetic time to extinction, where the initial conditions have an effect on the established phase, the initial conditions of the model do not have any consequences for the relaxation time (Grimm and Wissel, 2004). In addition to the mean time to extinction, the relaxation time (*Trel*) is also an important measure for models depicting viability analysis for certain species. The (*Trel*) specifies the period until the dynamics of the tiger population are no longer affected by the initial conditions of the model.

2.3 Modelling the Effect of Fragmentation on Population Dynamics

The rapid reduction of natural habitats and fragmentation has been motivating ecologists to understand the response of a population to these factors (Sutherland, 1996). The Metapopulation concept plays in an important tool for understanding the mechanism of biological consequences from habitat loss and fragmentation (Hanski, 1998; Fahrig, 2007a). Metapopulation was first modelled by Levin in 1969 to simulate colonization and extinction in the landscape (Fahrig, 2007a). The earlier metapopulation model assumed that landscapes consist of homogenous patches. The spatial realistic population model was recently developed to consider spatial heterogeneity. However, this approach is similar to the patch-occupancy model, which does not include population processes such as birth, death, emigration and immigration (Fahrig, 2002). The metapopulation dynamics suggests that the response of a population to habitat destruction is non-linear due to the nature of the destruction itself. The declining metapopulation also present a time lag and the amount of habitat is a key factor for long-term persistence (Hanski, 1998)

2.3.1 Landscape Representation

The spatial structure of a landscape where a species exist affects its population dynamics as much as birth, death, immigration, and emigration rates (Hanski, 1998). Models have been constructed to understand the mechanism of the effect of spatial structures on population dynamics. Particular attention placed on the representation of landscape in the models. In general, there are three categories of landscapes represented by the models, including the theoretical ecology, the metapopulation, and the landscape ecology (Hanski, 1998). Figure 2.5 illustrates the three approaches for the representation of landscape. The first category is the theoretical ecology approach which represents landscape as homogenous patches where individuals move between patches.

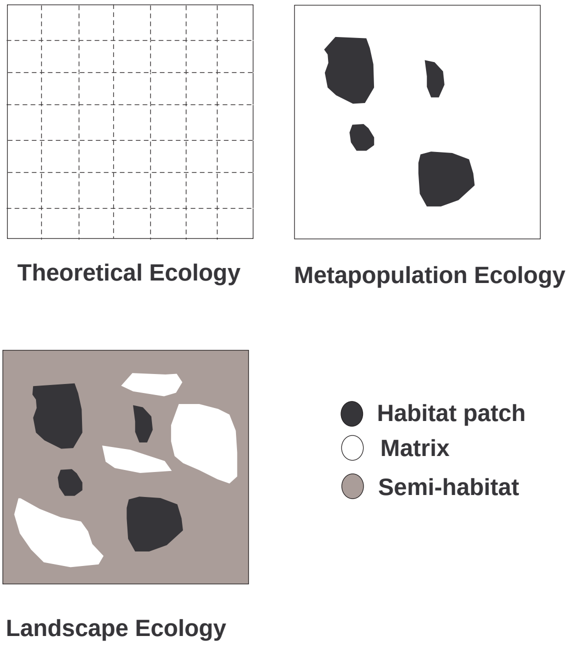


Figure 2.5: Landscape representations for theoretical ecology, metapopulation ecology, and landscape ecology. (A) is the landscape representation for theoretical ecology which consists of a homogenoues habitat. (B) is the metapopulation approach to represent landscape as discrete habitat patch and surrounded by a matrix, and (C) is the landscape ecology which represents landscape as patches with different qualities, involving habitat-matrix and semi habitat, re-drawn from Hanski (1998)

The second category is based on the metapopulation concept origining from Levin (Fahrig, 2007a). This category represents landscape as a networks of habitat patches occupied by discrete local populations. The original metapopulation only considered colonization and extinction rates in each patch to measure "occupied patches". Local populations dynamics such as birth, death, immigration and emigration are not considered (Fahrig, 2007a). Additionally, it assummes that all habitat patches have equal rates of colonization and extinction rates. Thus, the spatial structure in the early stages of the metapopulation is not explicit (Fahrig, 2007a). Within the same metapopulation ecology category, current developments in spatially realistic metapopulation model is considered to represent the spatial structure of landscape. The representation of landscape differs from previous category in two respects: patches are assumed to have different size and have relative location or distance from each other (Fahrig, 2007b). The third category is the landscape ecology, which also assumes that patches are characterized by size and relative location between them. However, this third category represents landscapes in much more complex manner; it not only considers habitat-patch distribution, but also the quality and pattern of the matrix (Fahrig, 2007a). Because the quality of the matrix varies in this category, the emigration rate is affected by the quality of matrix.

The importance of habitat/matrix quality and patterns have been highlighted to affect metapopulation dynamics (Moilanen and Hanski, 1998). As natural habitat is reduced with the presence of human-induced habitats, landscape representations also considers these changes. The habitat qualities are represented from simple good-poor-matrix (Wiegand et al., 2005) and a complex representation such as matrix-sink-refuge-attractive sink-source (Naves et al., 2003). Each habitat category represents the quality of habitat with respect to survival and reproduction. Matrix is the highest human effect and the lowest habitat quality, with no reproduction and/or very high mortality. Thus, this habitat category is avoided. The sink habitat type with presents reproduction and high mortality. Refuges have scarce nutritional value and low human interfere. Attractive sinks denote a habitat where a good habitat existed but animals poorly perceive the risks from humans. Attractive sinks has a high reproduction rate but also high mortality. Sources determines a high abundance of resource and low human effect and consequently have high reproduction and low mortality. Figure 2.6 ilustrates the habitat categories with regards to reproduction and survival approaches.

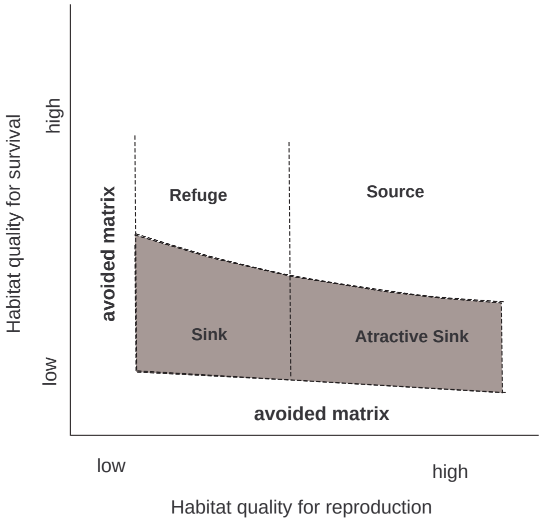


Figure 2.6: Source-sink diagram for large carnivores. Source is related to nutritional values of a habitat and sink is related to mortality by humans (re-draw from Naves et al. (2003))

2.3.2 Movement Ecology

Movement decisions on the individual level is known to affect the dynamics of a population (Kramer-Schadt et al., 2004; Cramer and Portier, 2001; Tischendorf, 1997). Animal movement, which is driven by spatial and temporal scale process, is fundamental behavior for determining the fate of an individual (Nathan et al., 2008). Additionally, movement rules have been recognized as critical features for determining the stabilization mechanisms in predator-prey systems (Hosseini, 2006). Therefore, understanding the causal mechanism of individual decisions to change environments is important for management decisions (Nathan et al., 2008).

Movement mechanisms are diverse among organism, varying from simple organism like microorganism to sentient organism such as large mammals and across different species, such as migratory birds, mammals, sea animals, etc. However, among this wide variety and diversity of movement, a unifying mechanism for individual movement produces movement paths, covering single step to lifetime tracks (Nathan et al., 2008). The proposed framework evaluates movement of individual through 2 main components, internal and external components. These two components are important factors for an individual's decicion to move or not. These can be formulated based on four aspects: the movement motivation (W), navigation capability (Φ), motion capacity (Ω), and external environmental conditions (R). The movement path (U) is a results of dynamics interaction between these four factors.

The internal state variable of an individual (W) is directly related to the motivation/goals of individual movement. The purposes of animal movement varies from acquiring resources, avoiding predators or competition, mating, and other social interactions (Fahrig, 2007b; Nathan et al., 2008). Motion capacity of individuals reflects its capability to move in various ways, based on biomechanical properties such as birds to fly, fish to swim, horse to run, etc. Navigation capability (Φ) is directly related to external environmental conditions (R). The individual's ability to orient its position, to identify where and when it should move, are integrated within these two factors. Figure 2.7 ilustrates the process of the movement decision for individuals.

2.3.3 Population Persistence of Endangered Animals

The Population Viability Analysis (PVA), as one modeling approach, plays an important part in the conservation of endangered animals. The purpose of the PVA can vary from providing central tendencies of population dynamics (Coulson et al., 2001) to estimating the probability of extinction for a population in the future while it can also assess the effect of management decisions and explore the consequences of uncertainty of assumption in parameters (Boyce, 1992; Coulson et al., 2001; Begon et al., 2006).

Three approaches have been commonly used during the PVA process: a) predicting the extinction through existing long-term population monitor-

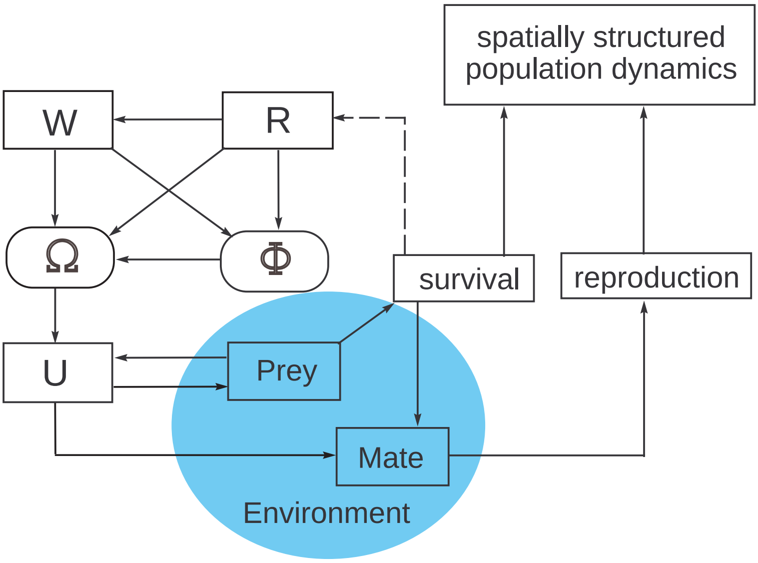


Figure 2.7: Movement decision process for individuals and its relation to the population dynamics of predator (modified from Nathan (2008); Revilla and Wiegand (2008)). W is the movement motivation which is driven by the internal conditions, Φ is the navigation capability, Ω is motion capacity, R is external environmental conditions, and U represents the path of movement. The R-external environmental condition affects navigation capability, motion capacity, and also internal conditions (W). U is the movement path which affects the interaction between an individual tiger with prey and mate. These relationships then affect individual survival and reproduction.

ing; b)subjective expert assessment; and c) the development of population models (Begon et al., 2006). Among those three approaches, the second is the most common approach used for extinction prediction and is developed through generic PVA models such as RAMAS, VORTEX and ALEX (Lindenmayer et al., 1995).

In principle, most PVAs which consider landscape are based on the metapopulation concept. The distinct difference between PVA and classical metapopulation is that PVAs include the population process in the patch, specifically birth, death, emigration, and immigration. However, in terms of landscape representation, most PVAs represent the landscape as homogeneous patches. PVAs only simulate habitat patches where each local population occupies a patch with a distinct size and distance from other local populations. Most PVAs exclude both the movement of the organism and dispersal mortality within the matrix (Fahrig, 2007a). Additionally, the effect of landscape configuration on individual movement decisions and population dynamics are poorly represented in most PVAs. Thus, any model being for population persistence should integrate landscape configurations (Russell et al., 2003). The importance of the ecological process and the consequences of interaction with other species, such as predator-prey, environmental fluctuation and variabilities, spatial structure of the population (e.g. spatial heterogeneity and dispersal), will benefit from the use of PVAs for the population persistence measure (Boyce, 1992)

The effect of fragmentation on the extinction thresholds can be demonstrated using two main simulation models (Fahrig, 2002): the colonization-extinction (CE) model and birth-immigration-death-emigration (BIDE models). Both models differ on the means of synthesizing the effect of fragmentation on the extinction thresholds, as result of the mechanism used to produce extinction threshold; CE has a higher extinction threshold than in the BIDE model. In the CE model, the effect of fragmentation is defined in the reduction of colonization rate, if the habitat is reduced. The BIDE assumed that the extinction threshold is affected by reduction in reproduction rate and increases mortality (Fahrig, 2002). This implies that in the BIDE model, the effect of habitat loss is more pronounced in the extinction threshold than in the threshold presented by the CE model. Conversely, population extinction can have a stronger influence in CE models.

2.4 Individual-Based Modelling of Population Persistence

The missing links between population ecology and behavioural studies emerge in the relational concept between individual behaviour and its consequence for population levels (Sutherland, 1996). The individual-based model was first recognized being used in ecology in 1960s. However, there is no current absolute definition of the concept (DeAngelis and Mooij, 2005; Grimm and Railsback, 2005). The rise in individual-based models in ecology was motivated by the fact that a population or a system consists of distinct individuals with adaptive trait and behaviours (Grimm and Railsback, 2005; DeAngelis and Mooij, 2005). Each individual seeks fitness through interactions between individuals and their environment and determine the properties of higher level such as population number, density etc. Individual-based modeling (IBM) tries to answer fundamental questions in ecology about how properties at the system level can be explained using individual adaptive traits (Grimm and Railsback, 2005).

IBMs offer advantages for handling complex individual traits and behaviours on a finer scale than classical or matrix models (DeAngelis and Mooij, 2005). The ability of IBM to include greater details for qualitative and quantitative individual traits have made this modelling approach better able to answer many ecological questions, in which require complex interactions between individuals and their environment (Grimm and Railsback, 2005; DeAngelis and Mooij, 2005; Grimm, 1999). In addition, the explicit expression of space among individuals in IBM contributed significant insight into local population variations in metapopulations which cannot be expressed in classical ecology (DeAngelis and Mooij, 2005).

Individual variations in the IBM are categorized as spatial, ontogenetic, phenotypic, cognitive, and genetic (DeAngelis and Mooij, 2005). Spatial variation among individuals is an important component for models involving animals which exhibit territorial behaviour (Wang and Grimm, 2007), foraging animals in the landscape (Russell et al., 2003), predator-prey relationships (Gergs et al., 2010), predator-prey-habitat relationships (Baeza and Estades, 2010) and predator-landscape relationship (Kramer-Schadt et al., 2004; Cramer and Portier, 2001). IBM can handle simulations which require fine details about individuals such as age, age structure, and sex identity, which represent ontogenetic properties of individuals (Jager, 2001; Ahearn et al., 2001; Rudolf, 2008). The phenotypic variation in the individual is important for population dynamics. Thus, modelling approach which accounts for individual phenotypic variations such as IBM provides a proper tool for mimicking real-life situations (DeAngelis and Mooij, 2005).IBM also has the ability to simulate animal's cognitive response to the presence of threats (Jaeger et al., 2005). This provides insight into the mechanism of individual learning processes. Finally, individual genetic information are important traits for long-term population dynamics. The fine details of individual variations involving loci - not only single locus such as in the classical model - is supported by the development of IBM (DeAngelis and Mooij, 2005). Such studies have used IBM to simulate the genetics of individuals in static and dynamic ways (Pertoldi and Topping, 2004).

Endangered species conservation has used IBMs as an approach for the population viability analysis (PVA). IBM was used to develop generic models for PVA, such as VORTEX and GAPPS (Brook et al., 1999). The developments of these models has encouraged the use of IBM for assesing many taxa, such as birds and mammals (DeAngelis and Mooij, 2005). Such individual-based PVA models were also developed to answer problems relating to specific species, including landscape configurations for lynx, Florida panther, and the Brown bear (Kramer-Schadt et al., 2004; Cramer and Portier, 2001; Naves et al., 2003), the effect of poaching (Kenney et al., 1995), and conflict with humans (Ahearn et al., 2001) affect on tiger populations. Thus, these examples provide evidence that IBM is a proper approach for predicting population persistence for general species, and also for specific species and problems.

2.5 Sensitivity Analysis in Individual-based Model

IBMs have improved classical modelling approaches through the inclusion of higher details about individuals and behaviours. However, at the same time this modelling approach demands an excessive amount of biological data which are difficult to obtain (Thornton et al., 1979; Mooij and DeAngelis, 2003; DeAngelis and Mooij, 2005; Grimm and Railsback, 2005). One of the fundamental processes in model development is the model analysis. This step involves various approaches and techniques, such as the robustness test, statistical analysis, sensitivity analysis, etc. (Drechsler, 1998; Grimm et al., 2006).

Ecological models are built under uncertainties which might come from values used in the parameters, parameterization of the system, choice of experiment, and stochasticity in the model (Cariboni et al., 2007). Thus, a sensitivity analysis is an important process for model development (Thornton et al., 1979; Crosetto et al., 2000), providing practical information that allows an understanding of the parameters that have the greatest effect on the outputs of the model, improving the model's precision, and indicating the reliability of the model's prediction (MacCarthy et al., 1995). Furthermore, sensitivity analyses might improve ecological models by investigating uncertainties in the parameters, enabling users to form an inference from the results, to understand the model itself, and to gain insight into the systems represented by the model (Cariboni et al., 2007; Grimm et al., 2006).

Sensitivity analysis methods vary with different approaches, ranging from local to global, and from quantitative to qualitative. Figure 2.8 presents the available sensitivity analysis approach for the ecological model as reviewed by Cariboni et al. (2007). Local approaches are kown as "one factor at a time (OAT)" are carried out by evaluating the effect of the change of a single factor and fixing all other factors at their nominal values. Global approaches evaluate the output of the model from a factor by varying all other factors. The global approaches allow for the identification of non-linear and/or non-additive interaction in the model's parameter. Unlike local approaches, global approaches do not require assumptions of additivity or linearity. However, the global approaches are usually computationally

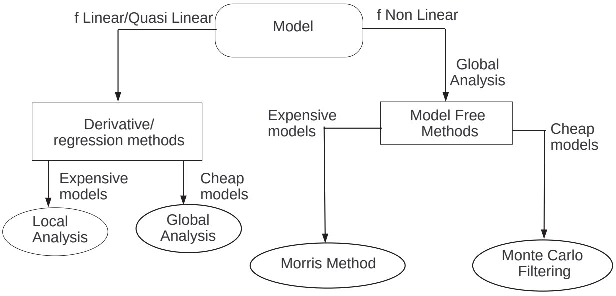


Figure 2.8: The diagram on main methods for sensitivity analysis in two major modelling function (f): linear/quasi linear and non linear (adopted from Cariboni et al. (2007)).

expensive, whereas the local approach is less expensive due to the number of simulations needed (Cariboni et al., 2007).

The qualitative methods are aimed to screen/select factors which are non-influential. These approaches only provide relative importance for factors that are evaluated and cannot be used to provide information on the relative difference of importance. Quantitative approaches are able to provide information about the amount of variance explained by each factor. The computational costs, similar to those for global and local approaches, for qualitative and quantitative approaches is one of the key factors during simulations. The qualitative approach generate a lower number of simulations, and therefore, the computational cost is lower than those created by quantitative approaches (Cariboni et al., 2007; Saltelli et al., 2006).

Chapter 3

Methods

Summary: The previous chapter described the theoretical basis for interpreting the results of this study. This chapter serves as a description of the methods. Section 3.1 describes the selected area for this study. Section 3.2 describes the Panthera Population Persistence (PPP) model. Section 3.4 describes the techniques being used for testing the PPP model and for assessing the data generated by the PPP model.

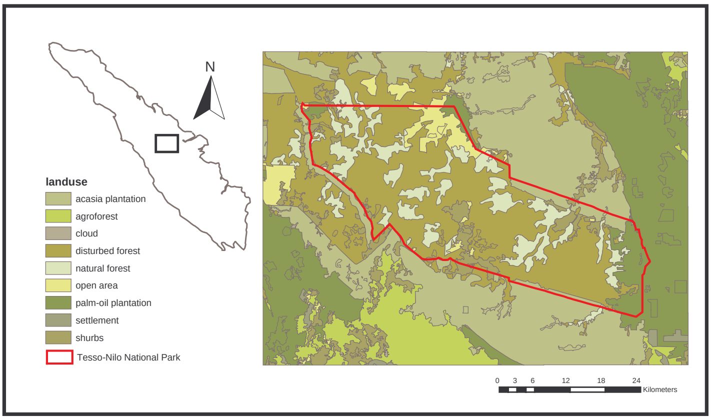


Figure 3.1: Map of the study area in the Tesso Nilo National Park and surrounding area, Riau province, Indonesia. Red line indicates the current park border. Each land-use type is represented by different colours.

3.1 Study Area

The Tesso Nilo National Park and the surrounding landscape, with a total size of 3,841 km^2, is situated between N. 00^{0}.03’.18" - S. 00^{0}.25’.34" and between E. 101^{0}.29’.17" - 102^{0}.8’.13", in the lowland area of Riau province of Central Sumatra, Indonesia. The park was established in 2004 and was formerly an area designated for logging concessions with a total area of 38,576 hectares, extended to 83,000 hectares in 2009. The current landscape configuration in the study area consists of various land-use types, such as natural forest, secondary forest, acacia plantation, palm-oil plantation, agriculture area, mixed forest, and settlement as illustrated in Figure 3.1.

3.2 Model Description

The Panthera Population Persistence (PPP) model was constructed to improve the existing TIGMOD model (Ahearn et al., 2001). The TIGMOD model was successfully implemented to simulate basic behaviour of tigers and potential tiger-humans conflict in Nepal. In the TIGMOD model, interaction between tiger, wild prey, and domestic prey was simulated in a spatially explicit way, but the long-term extinction prediction could not be assessed due to the use of a short time-horizon in the study. Additionally, the three trophic interactions between tiger-prey-habitats were not simulated. Thus, the model could not be used to assess the effect of landscape configuration on tiger population dynamics. The individual traits in the PPP model were improved through finer resolution of the state variables of tiger, prey, and habitat. These state variables are necessarily for simulating the trophic interaction between tiger-prey-habitat. The representation of landscape features is parameterized for the Tesso Nilo National Park and the surrounding landscape.

The description of the PPP model follows the ODD (overview, design concepts and details) protocol for describing individual- and agent-based models (Grimm and Railsback, 2005; Grimm et al., 2006). The PPP model is implemented in NETLOGO v. 4.1. (Wilensky, 1999). The model description in this chapter only focuses on the basic PPP model, whereas the modifications of the model used to address particular sub-questions in this study are explained in Chapter **??**.

3.2.1 Overview

Purpose

The main purpose of the construction of the PPP model is to investigate the effect of human threats and landscape configuration on the persistence of a Sumatran tiger populations.

States variables and scales

Individuals The PPP model comprises of three animal species: the Sumatran tiger (*Panthera tigris sumatrae*) and two of its prey species, the Sambar deer (*Rusa unicolor*) and the Red Muntjac (*Muntiacus muntjac*). Each tiger has different sex and age classes, hunger and starvation levels, and reproductive-based state variables. The Sambar deer and Red Muntjac have age and hunger levels. The Sambar deer represents large-bodied prey, which is preffered by tigers, but its population density is relatively low in Sumatra (O'Brien et al., 2003). The Red Muntjac have a relatively high population density in the Sumatran tropical forest (O'Brien et al., 2003) and represents a common small-bodied prey species for tiger on Sumatra island. Table 3.1 provides the description of state variables for each species in the PPP model.

Spatial Unit The PPP model can be used to simulate both artificial landscape and real landscape. The artificial landscape has a size of 203 x 149 grid cells, with each grid cell representing 12.7 hectares and is characterized by a habitat quality. The real landscape represents the Tesso Nilo National Park and surrounding landscape with a total size of 3,841 km^2. The size of this landscape is also represented by similar size as the virtual landscape in the PPP model. In addition, the habitat quality in the real landscape is represented by land-use types as illustrated in Figure 4.17.

Time Units As in the TIGMOD model, the time step in the PPP model is 0.5 days. This time step is important to demonstrate the interaction between individual behaviours such as movement and feeding (Ahearn et al., 2001). The time horizon for the model varies from 5-20 years, depending on the specific purpose for the model's use, with regards to the research questions as described in Chapter **??**.

3.2.2 Process Overview and Scheduling

Ageing

Tigers and prey increase in age with a time step of 0.5 days with age classes changing accordingly (Ahearn et al., 2001). Age classes and internal state conditions lead to different behaviour patterns, for instance cubs that only follow the mother or hunger levels which determine whether individuals will hunt or not. Figure 3.2 illustrates tiger behaviour for different age classes within the PPP model.

Table 3.1: Description and units for state variables of individuals in the PPP model

Individuals	State variables	Description	Values and units
Sumatran tiger	age	age of individuals	0-5,400 days (Sunquist et al., 1999; Smith, 1993)
	age-classes	classes of age	cubs (0-660 days)(Sunquist et al., 1999)
			sub-adult (660.5-825 days)(Sunquist et al., 1999)
			adult (825.5-5,400 days)(Sunquist et al., 1999)
			adult old (> 5,400 days) (Sunquist et al., 1999)
	sex	sex classes	male-female
	hunger level	energy level of an individual	0-100 (Ahearn et al., 2001)
	starvation level	starvation level of individual	0-30 (Ahearn et al., 2001)
	reproduction-related status	female state variable related to reproduction condition	fertile, infertile, pregnant, parent (Ahearn et al., 2001)
Prey	age	age of individuals	Sambar deer (0-6,120 days) (Nugen et al., 2001)
			Red Muntjac (0 - 3,600 days) (Chapman et al., 2005)
	hunger level	energy level of an individual	0-200 (Adjusted parameter)

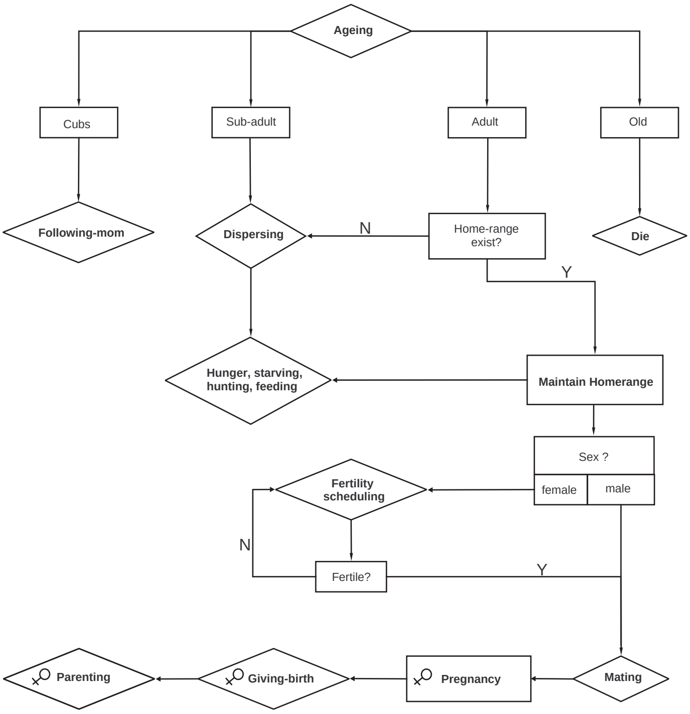


Figure 3.2: Conceptual diagram of main tiger behaviours in different age-classes within the PPP model. The age class determines the behaviour of an individual in relation to its internal states and environmental conditions. The submodel highlighted in bold are explained in detail in the process overview and scheduling.

Movement

The PPP model simulates two types of tiger movements: random and directed movement. If the movement of an individual does not target a specific object, it is considered to random movement. Tigers are known to have a wide geographical range, but also exhibit a site fidelity and territoriality (Miquelle et al., 1999a). Fidelity and territoriality in the PPP model was simulated through random movement while maintaining home range. Directed movement is driven by external factors which encourages an individual's decision to move such as following its mother, hunting, mating, and parenting, as outlined below.

Distances and directions of tiger movement refer to the individual movement in TIGMOD model (Ahearn et al., 2001). Appendix C shows the movement distance and direction for each behaviour exhibited by a tiger. The direction of movement is determined by random direction with persistence
$\alpha = \beta_1/(\beta_1 + \beta_0)$

with α being the probability of the decision to move to the next patch, β_1 representing the habitat index of the next path and β_0 denoting the habitat index of the current patch. A tiger moves to the next grid cell if the α value > 0.5, otherwise it will stay on the current grid cell. The PPP model simulated prey movement as random movement with persistence which is similar to tiger movement, and the distance of the movement is explained in the sub section sub model.

Hunger and Starvation

Hunger and starvation are important basic behaviours for representing interactions between tigers and prey. These two behaviour were successfully tested against the time interval between consecutive prey killed by tigers from an empirical study (Ahearn et al., 2001). In the PPP model, the hunger level of a tiger starts at 0 and increases by 10 per time step and by 12.5 for a tigress with cubs. If an individual has a hunger level above 90, starvation behaviour will begin. In this case, the hunger level is fixed to 90, and the starvation level increases by 0.5 per time step. If a tiger

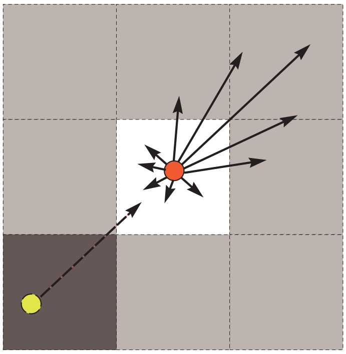


Figure 3.3: Random direction with persistence of tiger movement in the PPP model. White box represent current grid cell occupied, light grey boxes represent neighbouring grid cells, and dark grey represent previous grid cell. The dashed yellow circle and arrow represent position and direction of previous movement, respectively. The vectors represent the probability of the movement direction. The longer the vector, the higher the probability to move to the same direction (adapted from Ahearn et al. (2001)).

reaches a starvation level of 30 it will die. When hunger levels are >60, hunting is stimulated. The hunger levels of a tiger will decrease when it has successfully caught and consumed its prey; from this case the starvation level is returned to zero and the hunger level is reduced by 12.5 per time step over the entire feeding period. Figure 3.4 ilustrates the increment of hunger and starvation levels and their relation to hunting procedures in the PPP model.

Hunting

A tiger searches for prey within a specific hunting radius. When a tiger sense its prey, it will change direction accordingly. The hunting success rate of a tiger varies from 5% to 50% (Sunquist, 2010). The PPP model uses a conservative approach at the hunting success rate of 50% for any hunting occasion. Tigers prefer Sambar deer (Reddy et al., 2004), and if no Sambar deer is available within their hunting radius they will prey on Red Muntjac. Figure 3.4 shows the conceptual diagram of the process of

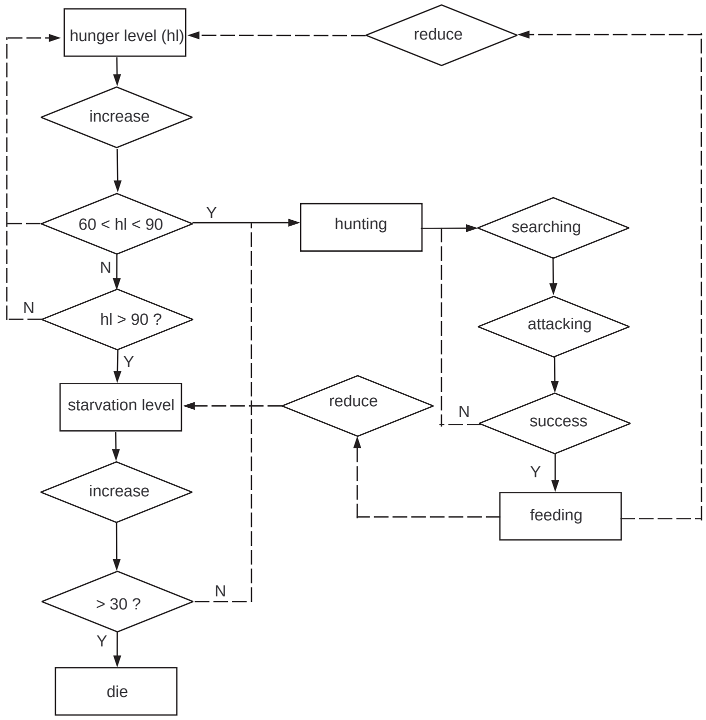


Figure 3.4: Hunger, starvation, hunting and feeding procedures in the PPP model.

hunger and starvation which ignites hunting behaviours.

Feeding

Tigers stay close to their hunted prey during feeding time (Sunquist, 1981); the larger the prey, the longer the tiger will stay to consume it. If a tiger successfully kills its prey in a tropical forest, the model simulates two consecutive days for consumption of a Red Muntjac and seven days for consumption of a Sambar deer, without interruption. Tigers spend less time consuming prey when kills are made in human-affected areas, as in undisturbed areas tigers are more likely to eat more meat and spend more time doing so (Kerley et al., 2002). To incorporate the effect of human-disturbed areas, the feeding time is adjusted into 1.5 days for Red Muntjac and 5 days for Sambar deer.

Reproduction

The PPP model simulates the tiger reproduction through three processes: fertility scheduling, mating, pregnancy and deliver cubs. A female reaches sexual maturity at the age of 825 days (Sunquist, 1981) and in the model fertility scheduling is initiated. The inter-estrous interval of a female tiger is around 25 days during which the female is fertile for about 5 days. A fertile female will call to an adult male for mating, but the PPP model did not simulate this call. Mating will only occur when individuals' hunger levels are lower than 60 and starvation is not present. The duration of mating is two days (Sunquist, 1981) and the female has a 50% chance of becoming pregnant. The gestation period for a female is 102-103 days (Ahearn et al., 2001; Sunquist, 1981; Sunquist et al., 1999). Tigers have disproportionate sex ratio during adulthood, 1:3 or 1:4 (Sunquist, 1981), but the ratio is also known to be at parity in zoos (Schaller, 1967), with an average litter size of 2.8 individuals (Sunquist, 1981; Schaller, 1967). The PPP model simulates a random probability of giving birth to 1-3 cubs with a ratio of males to females of 1:3. A new-born tiger will usually adopt all characteristics of its mother, except for sex class, age, and hunger and starvation levels. The age of cubs is 0 at the time step of birth. Hunger and starvation levels are also 0 until the cubs reaches sub-adulthood. A female with cubs will not display any mating behaviour until the cubs reach sub-adult classes. In the model, density dependent birth rates are simulated for both Red Muntjac and Sambar deer.

Mortality

Two types of mortality for tigers and prey were simulated in the PPP model, including natural mortality and human-induced mortality. The PPP model defines natural mortality of tigers and prey through ageing behaviours. Tiger and prey die if they reach their maximal life expectancy which is driven by ageing behaviour. In addition to natural mortality through ageing, prey mortality is also a result of tiger killing and natural mortality for tiger can be caused from an acute starvation. A tiger might die due to starvation if the starvation level reaches > 30. Human induced mortality is simulated by the effect of poaching on tiger and prey. If the dead tiger is a female with cubs, the cubs will also die. When an adult male or female tiger dies, the home range will be occupied by a sub-adult that is searching for a home-range.

Dispersal

At the sub-adult level, tigers search for a home range. The home range of a male may overlap with one or several females but never with the home range of another male. An adult individual without a home range is removed from the model but is not considered a dead individual. The PPP model calculates this as a dispersed individual.

3.2.3 Design concept

Emergence

The dynamics of the tiger population emerge from the interaction between individuals of tiger, prey and habitat.

Interaction

The PPP model explicitly simulates four types of interaction. The first is a prey-habitat interaction, which shows the movement and the foraging behaviour of prey in different habitat types, prey decides whether to move to the next patch or to stay depending on certain habitat indices. Such indices also determine the energy gained by the prey while foraging. The second type of interaction is a tiger-prey interaction, which represents the behaviour of a tiger hunting prey. The third type of interaction is tiger-prey-habitat, which represents the time taken to consume prey that has been killed on different land-use types. The fourth type is a tiger-tiger interaction, which simulates the behaviour of mating and parental care between a mother and cubs.

Adaptation

Tigers select medium and large prey when resources are abundant (Karanth and Sunquist, 1995; Biswas and Sankar, 2002), but tigers also are flexible to consume smaller prey if resources are scarce (Reddy et al., 2004). The PPP model simulates the tiger preference of Sambar deer. However, when there is no Sambar deer in the hunting radius, the tiger will prey on Red Muntjac. Newborn tigers inherit this preference for large prey. Adult tigers are known to compete for resources and mating (Sunquist, 1981). When an adult individual cannot establish a home range, the model considers it transient and removes it from the landscape. Tigers are able to detect prey and mates, and a cub senses the presence of its mother and the need to follow.

Stochasticity

Stochasticity is applied to the probability of a tiger to successfully hunt for prey, the probability of becoming pregnant, the number of new cubs, and the proportion of male to female cubs.

Collectiveness

Collectiveness occurs during mating and parenting behaviours. A male and a female will remain together throughout the mating period, and a female will stay with its cubs until they reach the sub-adult class.

3.2.4 Details

Initialization

Detailed initializations of the Sumatran tiger, prey, and habitat, are described in Chapter **??**.

Input

As a means to evaluate habitat quality and landscape composition (Sections 4.2 and 4.4), the PPP model used virtual and real landscape. These maps were generated from Arc GIS 9.1 and entered into the PPP model. The real landscape is based on the land-use map of the Tesso Nilo National Park and the surrounding landscape.

Observation

The observation of the outputs of the PPP model depend on the specific purpose of the model as shown in Chapter **??**. For example, for the purpose of sensitivity analysis, the number of tigers, dispersed tigers, total prey, and total prey eaten were monitored.

Submodels

The submodels in the PPP model include four main types of prey behaviours; movement, foraging, reproduction, and mortality. Details on these submodels are presented in Chapter **??** section 4.4.

Prey Movement As it is difficult to uncover any studies about the movement behaviour of Sambar deer and Red Muntjac on Sumatra island, the PPP model simulates the movement of both prey according to herbivores modes of movement (Fryxell et al., 2008). Prey movement is defined by two main factors, direction and distance. Distance refers to data obtained for red deer movement which varies from 0.23 - 7 km/day. This variation covers both the encamped mode (more sedentary behaviour) and exploratory mode (rapid directional movement)(Fryxell et al., 2008). The movement direction of prey is set similar to movement of tigers (above), except when it being tested as demonstrated in Section 4.2 of Chapter **??**.

Foraging behaviour of prey The foraging behaviour of prey is driven by the hunger level of an individual. Red Muntjac and Sambar deer hunger behaviour is simulated by increasing their hunger level by 10 levels per time step. As there is currently no data available about the rate of consumption for prey species within different habitat types, the same rate was used for all types of habitats. The presence of human-affected areas can increase the energy consumed by an animal in order to avoid human contact (Kerley et al., 2002). Prey will remain in a patch and consume a certain amount of the food resource in that particular patch. Prey will receive different resource values in different land-use types. At the same rate of increased hunger level, the greater the human intervention, the lower the level of energy gained from the patch, and consequently the more easily the prey becomes hungry.

Prey Reproduction Red Muntjac start to reproduce annually from the age of 2 to 4 years with the probability of the number of litters consisting of 3 individuals. Sambar deer annually reproduce with 1 litter from the ages 2 to 6 years. Both prey die when they reach a maximum age (approx. 10 years for Red Muntjac and 17 years for Sambar deer), from acute starving (hunger level is greater than 200), and/or are killed by tigers. Both Sambar and Red Muntjac have density-dependent birth rates. Both will continue to reproduce until the population reaches the carrying capacity.

3.3 Land-use Map Development

The land-use map was derived from a satellite image of LANDSAT (Path 126 row 60 date 07 August 2005). The land-use classification was manually completed from the satellite image and classified five land-use classes: relatively-natural forest, degraded forest, plantation, open area, and settlement. To adjust the map to the current situation of the study area, the map was then synchronized with a land-cover map from WWF-Riau (Uryu et al., 2007) and a ground check was conducted in November and December, 2009. The reclassification of the land-use map fallen into six major land-use types: tropical forest, secondary forest (logging concessions), agroforestry, acacia (*Acacia mangium*) plantations, palm-oil plantations, and settlements. Figure 3.1 displays the land-use classification of the study area within Tesso Nilo National Park and surrounding area.

Table 3.2: Proportion of the size of each land-use type in Tesso-Nilo National Park and surrounding landscape

Land-use types	Size (km^2)	Proportion from total (%)
Tropical forest	259.171	6.75
Logging concession	987.465	25.71
Agroforest	271.197	7.06
Acasia plantation	1086.53	28.28
Oil-palm plantation	836.144	21.77
Acasia Settlement	400.879	10.44
Total	3841.386	100

Table 3.2 describes the size proportion of different land-use types in the study area.

3.4 Model Analysis

3.4.1 Sensitivity Analysis

In order to identify a subset of parameters in the PPP model that significantly affect the output of the model, a screening method of sensitivity analysis was used. The screening method is a qualitative approach for a sensitivity analysis. This approach is very useful when the number of input factors is high (several tens or higher) and/or the model is computationally expensive. This method is computationally cheaper, model free, and can be used to identify non-influential factors (Cariboni et al., 2007; Saltelli et al., 2004; Campolongo et al., 2007). However, the drawback of the screening method is inability to quantify how much a given factor is more important than another (Saltelli et al., 2004).

The screening method involves a simple "one factor at a time (OAT)" technique, which varies one factor per simulation run to observe the variation in the output. The OAT also known as a local approach in sensitivity analyses. The main principle of this technique is to observe outputs that occur as the effect of a variation in a single factor, while all other remain fixed at their nominal values(Cariboni et al., 2007). Among the screening design, the Morris method is not only considered to be a computationally cheap technique, but it is also model free and can be used to identify non-influential factors and factor fixing settings (Cariboni et al., 2007; Saltelli et al., 2004; Campolongo et al., 2007). The principle of the Morris method is to evaluate which parameters may be considered important or negligible, linear and additive or nonlinear and those that may interact with other parameters (Morris, 1991; Campolongo et al., 2007).

In the Morris method, each input factor may vary over p levels and r trajectories which are randomly generated. Each trajectory is designed so that all factors are varied, one at a time across their levels. The Morris method computes the elementary effect of factor i (d_i) as follows:

$$\mathrm{d}_i(\mathrm{x}) = \frac{y(x_1,\ldots,x_{i-1},x_i+\triangle,x_{i+1},\ldots,x_k)-y(x)}{\triangle}$$

where $\triangle$ is a predetermined multiple of $1/(p\text{-}1)$, x = x1,x2,...xk is the selected point in the trajectories, and ($\mathrm{x}+\mathrm{e}_i\triangle$) is the transformed point where only the component i has been changed (Cariboni et al., 2007). Morris proposes two sensitivity measures for each factor; a measure μ that estimates the overall effect of the factor on the output, and a measure δ accounts for all the effects of a factor that are non-linear or due to interactions with other factors (Saltelli et al., 2004). The μ is the mean and the δ is the standard deviation of the absolute value of the elementary effect over the r trajectories. The experimental design of the Morris method includes randomized OAT experiments which were run using the Simulation Environment for Uncertainty and Sensitivity Analysis (SIM-LAB) version 2.2 (SIMLAB, 2010). The computational cost of the Morris experiment is a linear function of the number of factors (k), C = r(k + 1).

3.4.2 Survival Thresholds

This study introduces a new measure for conservation of endangered species: "*survival threshold*". The survival threshold provides a quantitative measures for predicting the effect of different factors such as poaching, level of human-tiger conclicts and habitat amounts, for the population persistence. The measurement of survival threshold ($P_S thresh$)is calculated by projection of factors being evaluated and the probability of extinction for a certain time horizon (P_0(t)). The P_0(t) represents a ratio between the numbers of simulations resulting in extinction and the total number of simulations. The $P_S thresh$ is defined within the interval $0.95 \leq P_0(t) \leq 0.99$, and projected into the value of the parameters being tested (See Fig. 2.4 for details).

3.4.3 Time to Extinction

The measures of the time extinction for this study include the arithmetic mean time to extinction (*Tavg*), the intrinsic mean time to extinction (*Tm*), and the relaxation time (*Trel*). The arithmetic mean time to extinction requires a simple calculation by averaging the times when a population experiences extinction as a result of simulations. The calculation of the intrinsic mean time to extinction (*Tm*) follows the protocol developed by Grimm and Wissel (2004) as outlined in the following paragraph.

The PPP model recorded the time step when absolute or quasi-extinction occurred within a certain time horizon (e.g. 20 years) using 100 repetitions. A histogram of extinction time was developed only for simulations which resulting in extinction. Thus, the histogram is divided by the total number of simulations, and then a plot of cummulative probability of the population becoming extinct P_0(t) by time t was developed. The -ln(1-P_0(t)) is then calculated and projected versus time step. *Tm* is the slope of the linear regression line based on the ln (1- P_0(t)) plot. The the relaxation time (*Trel*) specifies the period until the dynamics of the tiger population are no longer affected by the initial conditions of the model. The *Trel* is derived from the intercept of the regression line of -ln (1-P_0(t)) with the x-axis. The calculation of *Tm* and *Trel* were not carried out if the P_0(t) was very low. Figure 3.5 demonstrates the histogram of time to extinction and the projection of -ln(1-P_0(t)) across time step for the calculation of the *Tm* and *Trel*.

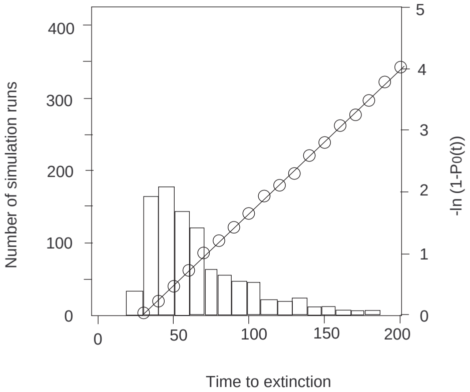


Figure 3.5: The frequency of simulation runs resulting in extinction in each time step (histogram) and plot of -ln(1-P_0t) at each time step to be used to measure of intrinsic time to extinction. The intrinsic time to extinction is the inverse of the slope of plot of -ln(1-P_0t) vs time step. *Trel* is based on the intercept of the regression line of -ln (1-P_0(t)) with the time (Grimm and Wissel, 2004)

Chapter 4

Results

Summary: The results of this study reflect two main processes for modelling development; analysis and application. Section 4.1 provides an evaluation of overall parameters employed in the PPP model through sensitivity analyses and comparison with other predator-prey model. Section 4.2 estimates and justifies parameters which were evaluated in the previous section by comparing the model's performance with existing data on the tiger-prey relationship. The applications of the PPP model for the conservation of the Sumatran tiger population are rendered in two different sections. Section 4.3 ilustrates the use of the PPP model to investigate potential extinction after the removal of Sumatran tiger poaching. Section 4.4 demonstrates the application of the PPP model to provide an understanding of the effect of landscape composition on the Sumatran tiger population dynamics.

4.1 Structure and Sensitivity Analysis of Individual-based Predator-Prey Models

Muhammad Ali Imron, Andre Gergs, Uta Berger

Summary: This section demonstrates an important step in the modelling development process: model analysis. This section highlights the importance of sensitivity analysis for understanding the behaviour of the outputs of the PPP model stemming from a change in input parameters. The results from the sensitivity analysis provide basic information about the relative effects of all parameters on the model's outputs and provides an insight into the predator-prey systems.

A slight modification of this section was submitted in the *Journal of Reliability Enginering and System Safety*, 15 October 2010, Manuscript Number RESS-D-10-00483. An earlier version was published in the Procedia-Social and Behavioral Sciences, Sixth International Conference on the Sensitivity Analysis of Model Output, 2010, Volume 2, Issue 6, pages 7680-7681, DOI: 10.1016/j.sbspro.2010.05.176

Abstract The expensive computational cost of sensitivity analyses has hampered the use of these techniques for analysing individual-based models in ecology. A relatively cheap computational cost, referred to as the Morris method, was chosen to assess the relative effects of all parameters on the model's outputs and to gain an insight into predator-prey systems. The structure and results of the sensitivity analysis of the Sumatran tiger model - the Panthera Population Persistence (PPP) and the Notonecta foraging model (NFM) were compared. Both models are based on a general predation cycle and designed to understand the mechanisms behind the predator-prey interaction being considered. However, the models differ significantly in their complexity and the details of the processes involved. The results from the PPP model displayed that the parental-care time duration, the hunting radius, and the growth rate of prey were the most influential parameters for the number of tigers and the prey killed, the number of dispersed tigers, and the remaining prey, respectively. The attack rate parameters of backswimmers were responsible for the fluctuation in the number of daphnid eaten in the backswimmer model. The findings highlight the importance of the sensitivity analysis, and in particular the screening design for early development of any individual-based models. Furthermore, the model's structure comparison and sensitivity analysis provide insight into predator-prey models for both practical conservation and conceptual understanding.

4.1.1 Introduction

Predator-prey interaction is one of the classic ecological issues that has been extensively described by mathematical models and increasingly simulated by means of spatially-explicit computer models. This interaction is frequently described as numerical responses at the population level and as functional responses at the individual level. For the latter, the Holling Type II function (Hinrichsen, 2009),which is adequate for many real species (Real, 1977; Jeschke et al., 2002), is most commonly applied in the mathematical description, but also has also been adapted to simulation models.

Current developments in Individual-based models (IBMs) in ecology have opened up new opportunities for testing the suitability of the predator-prey interaction concept for gaining insight into predator-prey systems and for practical conservation (Grimm, 1999; DeAngelis and Mooij, 2005; Grimm et al., 2006). IBMs have been used to understand emergence at the population level as results of individual traits, for example population dynamics arising from food availability in water flea (Preuss et al., 2009) or individual home-range maintenance behaviour (Wang and Grimm, 2007), have also been employed for predicting the persistence and the conservation planning of the Iberian lynx (Kramer-Schadt et al., 2004), tiger (Ahearn et al., 2001), and the Florida panther (Cramer and Portier, 2001).

One of the fundamental processes in the development of IBMs is model analysis. This step involves various approaches and techniques such as the robustness test, statistical analysis, sensitivity analysis, etc. (Grimm et al., 2006). In spite of the large number of studies employing IBMs for ecological and evolutionary processes that have been published in the last two decades (DeAngelis and Mooij, 2005), very few have been concerned with evaluating individual-based models by means of sensitivity analyses. In fact, sensitivity analyses might improve ecological models by investigating uncertainties in the parameters, helping us to take inference from the results, to understand the model itself, and to gain insight into the systems represented by the model (Cariboni et al., 2007; Grimm et al., 2006).

IBMs sometimes involve many uncertain parameters during model development. To identify those parameters, which will have a major influence on the output of a model, the sensitivity of selected parameters is usually tested using the traditional "one factor at a time"(OAT) method (Saltelli et al., 2006). For example, Karanth and M.Stith (1999) and Nilsson (2001) tested the effect of prey density and size on the dynamics of predator population or predation behaviour, while MacCarthy et al. (1995) studied the effect of fecundity and the initial number of birds on the population viability of the helmeted honeyeater (*Lichenostomus melanops cassidix*). A comprehensive sensitivity analysis of all parameters is considered to be a computational process that is not feasible for complex IBMs. Therefore, this kind of analysis is only recommended for relatively simple IBMs (Grimm et al., 2006). In addition, the use of the sensitivity analysis for IBMs have been neglected due to missing links between the purpose of IBMs and the inferences taken from the results of sensitivity analysis, as well as the usefulness of robustness tests for IBMs (Grimm et al., 2006).

Sensitivity analysis methods vary with different techniques, ranging from local to global and from quantitative to qualitative sensitivity analysis. Among these techniques, screening methods have been recommended to deal with highly complex models (Morris, 1991; Cariboni et al., 2007). In the study presented, the importance of sensitivity analysis as a crucial part in the early development of any individual-based ecological models is addressed. Two different model complexities were chosen to find similarities, to demonstrate a manageable method of sensitivity analyses, and to gain insight into predator-prey models.

4.1.2 Model Descriptions

The main similarities and differences between the two predator prey models are described following the ODD protocol as suggested by Grimm et al. (2006). The first example is the Panthera Population Persistence (PPP)- a relative complex predator-prey model, describing the population dynamics of Sumatran tigers and their prey, the second is the NFM model- a less complex model, describing the interdependent dynamics of the backswimmers *Notonecta maculata* foraging on their zooplankton prey *Daphnia magna.* The details of the PPP model is provided in Appendix A. The processes, equations and parameters of the Notonecta model have been published (Gergs and Ratte, 2009; Gergs et al., 2010) and a brief description is also provided in Appendix B .

Purpose, State Variables and Scale

The major purpose of the two individual based models is to understand the potential mechanisms behind the specific predator-prey interaction. Moreover, the PPP model is designed in order to understand the factors determining the population persistence of the Sumatran tiger, using parameterizations of Tesso Nilo National Park on Sumatra Island. Based on laboratory studies, the purpose of the backswimmer model is to assess and quantify the role of predators foraging on the population dynamics of the backswimmer *Notonecta maculata* and its zooplankton prey *Daphnia magna*.

Within the two models, all individuals of both predator and prey are characterized by a number of state variables at the start of the simulation. The population dynamics of the Sumatran tiger and two prey species, Sambar Deer and Red Muntjac, are simulated in the PPP model. The individuals of Sumatran tiger are differentiated by sex, age, age-classes, hunger level, starvation level, and the reproduction-related status for female tigers. Individuals of Sambar Deer and Red Muntjac differ in age classes. Properties of *N. maculata* are instar, encounter distance as well as attack- and success-coefficients. *Daphnia magna* properties are body length and the corresponding size class. The probability of attack and success as well as the time spent handling prey depend on the body length of the encountered daphnid. Brief descriptions of the parameters used in the PPP and NFM are given in Table 4.1 and Table 4.2, respectively.

The PPP model is mainly based on the earlier model of TIGMOD (Ahearn et al., 2001) for factor parameterization. In spite of the attractiveness of the Sumatran tiger for conservation, this species lacks of behavioural studies which are important for developing IBM. By contrast, backswimmers are less attractive from a conservation point of view and yet this species has been comprehensively studied through empirical studies and models. Hence, the behavioural data of this species is much more better than that available for the Sumatran tiger.

Process Overview and scheduling

The PPP model and the NFM involve similar key aspects of predation behavior as shown in the figure 4.1 . The foraging processes are described on the basis of a general predation cycle including four conditional events (searching, attack, capture success, and handling) as suggested by Gerritsen and Strickler (1977), instead of using classic functional response curves. Within the predation cycle, the predator starts searching or waiting for prey. An encounter between predator and prey is followed by an attack. In case of capture success, the predator starts feeding during a certain handling time. Rates of attack in the PPP model are determined by hunger level, whereas in the NFM these are defined by stochastic probabilities. Both models determine the hunting success through stochastic probabilities.

Despite differences in ecosystems and predator characteristics, both models take the distances between predator and prey into account in a similar manner: an attack might occur whenever a prey item enters the predators hunting range. As an active predator, tigers actively search for prey and are capable of detecting prey populations within a hunting radius. As a "sit and wait" predators, backswimmers usually attack prey found within a perceptive area from perch sites. However, the two models slightly differ in the formulation of the hunting radius or the encounter distance. The PPP model computes the distance between tiger and prey in a spatially explicit manner, whereas in the NFM, distances are empirically included in differential equations within the Notonecta model.

Besides the similarities in the foraging processes, both of the models differ in the overall behaviour of how predation affects the output of the model. Within the PPP, important behaviour is considered for every age-classes, except for predation behaviour, which is only simulated in sub-adults and adults; cubs have to follow the behaviour of the mother. In the Notonecta model predation is simulated for all of the five instars during larval development.

Design concepts

The ability of individual tigers to detect other individuals (prey for subadults and adults, mates for adults, and mother for cubs) and the environmental conditions leads to changed states in individuals. Accordingly, changed states in individuals directly lead to different behavior. Output of the model are the total number and dispersal of tigers, the total number of prey and the prey killed by tigers within a 5-years time horizon.

Individual backswimmers are able to sense daphnid prey and environmental conditions. The probability of attack and success as well as handling

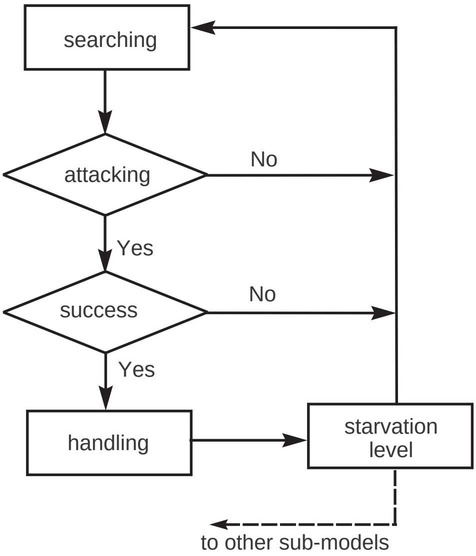


Figure 4.1: The key predation behaviour in the PPP model and the NFM which is driven by the change in the state of starvation level. The predation behavior leads to other sub models such as mating behaviour for the PPP model.

time depends on the size of the prey encountered. Except for predation no interactions between individuals are considered and population dynamics do not emerge from any properties of the individuals in the current state of the model. The predation behavior of backswimmers is expressed in empirically-derived, differential equations which are formulated as submodels and include a set of instar-specific parameters. For model analysis the prey killed within 3 hours was recorded.

4.1.3 The Sensitivity Analyses

In order to identify a subset of parameters that significantly affect the output of the models, screening design methods were used, which are known for their low computational effort. As an output, these approaches provide qualitative ranks of parameter importance for the model evaluated (Saltelli et al., 2004). The screening method involves a simple "One Factor At a Time (OAT)" technique, which varies one factor per simulation run to observe the variation in the output.

Morris (1991) suggested an OAT technique based on the computation of each input parameter with a number of incremental ratios, called elementary effects, which are averaged to assess the overall importance of the input. This technique is referred to as the Morris method hereafter. The principle of the Morris method is to evaluate which parameters may be considered important or negligible, linear and additive or nonlinear and those that may interact with other parameters (Morris, 1991; Campolongo et al., 2007). For each of the input parameters two sensitivity measures are computed: μ estimates the overall influence and δ estimates the higher order effects of the given parameter, i.e. interactions with other parameters and/or its non-linear behavior. Details described in Morris (1991).

The experimental design of the Morris method includes randomized OAT experiments which were run using the Simulation Environment for Uncertainty and Sensitivity Analysis (SIM-LAB) version 2.2 (SIMLAB, 2010). For the analyses 4 random levels were chosen from 29 parameters to generate 150 experimental samples in the PPP model. For the backswimmer model, 8 levels were chosen from 13 parameters and generating 70-sample experiment. Because the PPP model has multiple outputs, the most influential factor was identified by scoring approach as suggested by Campolongo et al. (2007).

Further sensitivity analyses of selected parameters were carried out, in order to gain an insight into predator-prey systems. Parameter values were gradually changed to test their effect on the output of interest in the models. Significant changes in the model outputs were tested by the Kruskal-Wallis test and Mann-Whitney U test using SPSS 11.5 in order to identify the ranges of parameter values which were relatively insensitive to changes. Both models were simulated by gradually changing the most important parameters, following plausible values. Other less influential parameters were fixed according to existing studies.

In the following section, the results of the sensitivity analyses as conducted for the PPP and NFM are shown separately before comparing the influence of hunting distances on the output of the two models.

The PPP model

The outputs parameters of the PPP model were sensitive to different input parameters. The number of tigers and the prey killed were sensitive to the time required by tigresses to take care of their cubs (T_{fol}), the number of dispersed tigers was highly influenced by a change in the hunting radius (Ht_{rad}) values, and the number of prey was sensitive to the growth rate of Red Muntjac (G_m).

Figure 4.2 shows the plot of μ and δ values of every input parameter affecting the output parameters of the PPP model. The order in the graphs corresponds to the relative importance of each parameter to interested outputs. The T_{fol} is shown at the top of plot μ and δ values for the number of tigers, but the separation with other parameters is not as clear as for the number of prey killed. The μ and δ values for Ht_{rad} are displayed as the highest from all parameters in the term of numbers of dispersed tigers. However, other parameters do not show a clear separation between each others. The G_m in the graph for the number of prey is clearly shown to

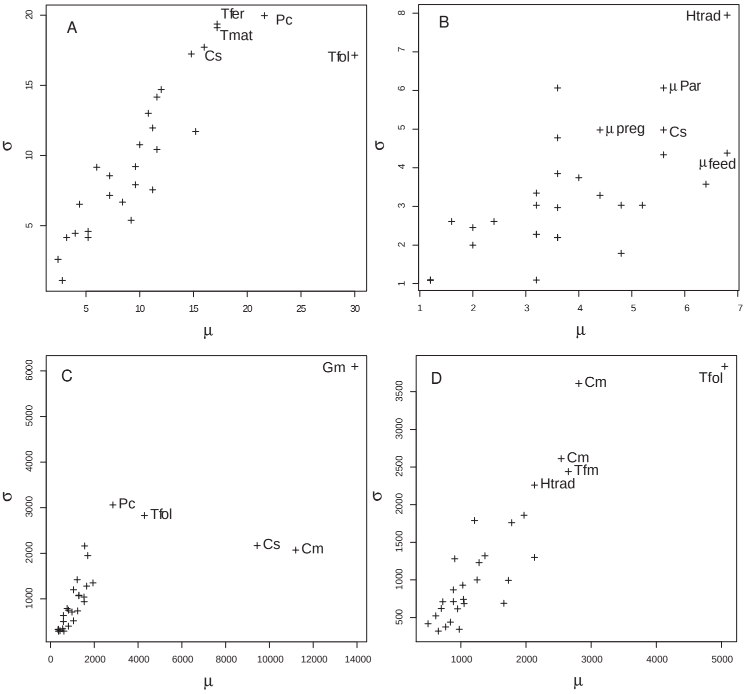


Figure 4.2: The plot of μ and δ values of all input parameters into different output parameters of the PPP model (A: total number of tigers; B : the number of dispersed tigers; C : the total prey numbers; D : the total prey killed by tigers)

be separated from other parameters, indicating that this parameter highly influences the output.

The Table 4.1 shows the scores and ranks of all parameters affecting the overall outputs in the PPP model. The 10 most influential parameters in the model were selected to gain a greater insight into predator prey-interaction. Among those parameters selected, Ht_{rad} was introduced in the PPP model after being adaptated from the TIGMOD model and is the only unknown parameter for tigers.

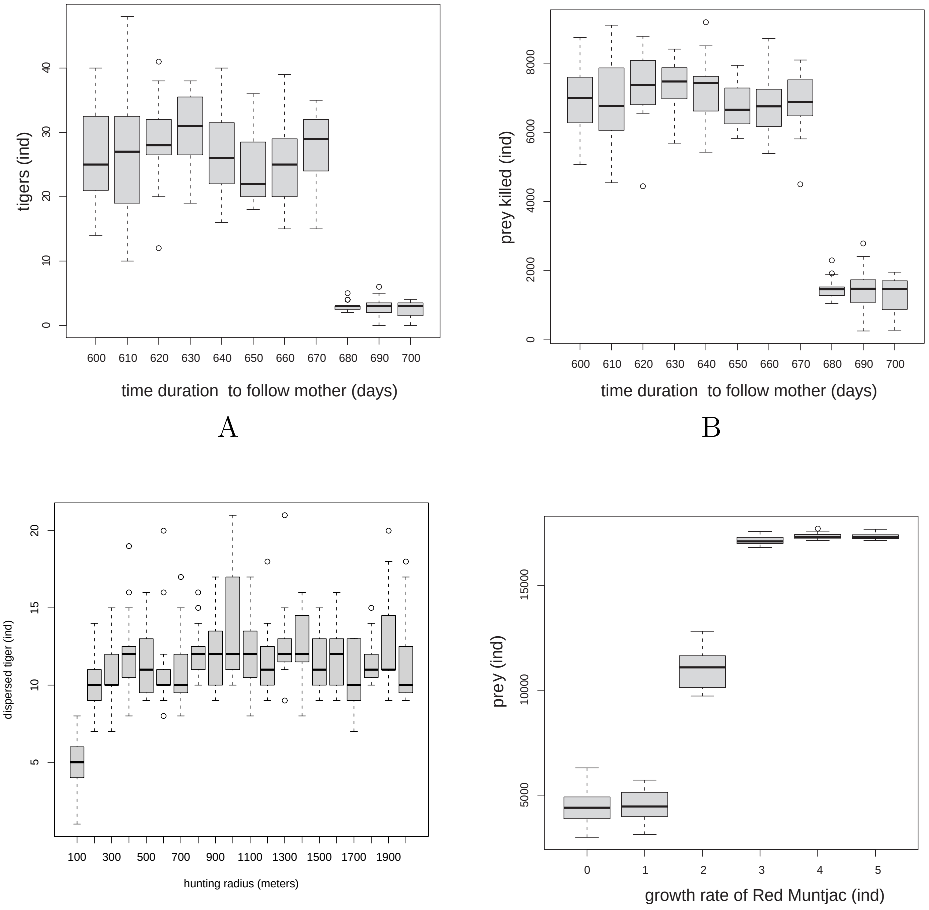
To test the effect of the most important parameters for each output variables, gradual changes to those parameters were evaluated against the output. A non-parametric comparison tests showed a significant difference for the number of tigers (Kruskal-Wallis, H= 101.89, $p < 0.01$) and the number of prey killed (Kruskal-Wallis, H= 101.99, $p < 0.01$) when a change was made for T_{fol} from 600-700 days. Dispersed tigers showed a significant difference (Kruskal-Wallis, H= 71.98, $p < 0.01$) when Ht_{rad} was gradually changed from 100 meters to 2,000 meters. The total number of prey at the end of simulation also showed a significant difference (Kruskal-Wallis, H= 76.36, $p < 0.01$) if G_m was changed from 0 to 6 individuals. Figure 4.3 shows the boxplot diagram of the effects of those three parameters on the output of the PPP model. The number of tigers are relatively stable at the values of T_{fol} below 670 days, and suddenly were dropped at values above 670 days. A similar pattern can also be seen for the number of prey killed by tigers. The number of prey killed abbruptly changed for the values above 670 days. The number of dispersed tigers are shown to be sensitive to the change of a Ht_{rad} up to 700 meters, and relatively insensitive for values above that. The number of preys were shown to be sensitive at the values of G_m betwen 1 and 3, and relatively insensitive for the values of 0 and 1, as well as for 3-5 individuals.

The NFM

The relative sensitivity of the parameters as calculated for the output of the NFM are shown in Figure 4.4. Additionally, values of μ and δ determined for each of the parameters are given in Table 4.2. Two parameters, *Aa* and *Ax0*, were detected to have relatively strong effects on the fluctuation in the number of prey killed compared to other parameters and thus considered to be the most important parameters for the NFM. Within the model framework, these two parameters are used to calculate the probability of attacking a particular prey item. This attack rate is formulated as a log-normal function of the prey size for each of the five Notonecta instars. The parameter *Aa* is a proportionality factor determining the maximum attack rate, whereas *Ax0* is the prey size corresponding to the maximum attack rate, i.e. the prey size which is preferentially attacked. Furthermore, a

Table 4.1: The ranks of the influential parameters in the PPP model after the sensitivity analysis and scoring approach. The values and Units are based on available studies, and if not indicated, adjusted parameters are used.

Parameter name	Description	Values and Units	Ranks
A_{mat}	Maturity age	825 days (Sunquist et al., 1999)	28
C_m	Initial density for Red Muntjac	2.2 ind/km^2 (O'Brien et al., 2003)	5
C_s	Initial density for Sambar deer	1.4 ind/km^2 (O'Brien et al., 2003)	4
G_m	Growth rate of Red Muntjac	2-3 ind/km^2 (Chapman et al., 1997)	8
G_s	Growth rate of Sambar deer	1 ind/km^2 (Semiadi et al., 1994)	13
H_{fem}	Female Home-range	70km^2 (Franklin et al., 1999)	23
H_{male}	Male Home-range	116km^2 (Franklin et al., 1999)	14
Ht_{rad}	Hunting radius of tigers to detect the presence of prey	1,000 m^2 (Adjusted)	6
P_c	Probability of successfull hunting	50 % (Sunquist, 2010)	2
P_{preg}	Probability to pregnant	50 % (Adjusted)	21
T_{fer}	Time duration to switch fertility status	25 days (Sunquist, 1981)	17
T_{fm}	Time duration to feed Red Muntjac	1-3 days (Sunquist, 1981; Sunquist et al., 1999)	7
T_{fol}	Time duration for cubs to follow their mother	660 days (Sunquist, 1981)	1
T_{fs}	Time duration to feed Sambar deer	7 days (Sunquist, 1981; Sunquist et al., 1999)	12
T_{mate}	Time duration for mating	2 days (Sunquist, 1981; Sunquist et al., 1999)	28
μ_{feed}	Mean rate of movement distance during feeding	400 m/day (Ahearn et al., 2001)	9
μ_{fer}	Mean rate of movement distance during fertile	1,000 m/day (Ahearn et al., 2001)	19
μ_{hunt}	Mean rate of movement distance during hunting movement	1,000 m/day (Ahearn et al., 2001)	24
μ_{mat}	Mean rate of movement distance during mating	3,000 m/day (Ahearn et al., 2001)	10
μ_{par}	Mean rate of movement distance during parenting	1,500 m/day (Ahearn et al., 2001)	3
μ_{preg}	Mean rate of movement distance during pregnancy	2,000 m/day (Ahearn et al., 2001)	26
μ_{rand}	Mean rate of movement distance during random movement	2,000 m/day (Ahearn et al., 2001)	11
σ_{feed}	Standard deviation of movement distance during feeding	400 m/day (Ahearn et al., 2001)	15
σ_{fer}	Standard deviation of movement distance during fertile	1,000 m/day (Ahearn et al., 2001)	25
σ_{hunt}	Standard deviation of movement distance during hunting movement	1,500 m/day (Ahearn et al., 2001)	16
σ_{mat}	Standard deviation of movement distance during mating	1,000 m/day (Ahearn et al., 2001)	29
σ_{par}	Standard deviation of movement distance during parenting	800 m/day (Ahearn et al., 2001)	18
σ_{preg}	Standard deviation of movement distance during pregnancy	1,000 m/day (Ahearn et al., 2001)	27
σ_{rand}	Standard deviation of movement distance during random movement	2,000 m/day (Ahearn et al., 2001)	20



A

B

C

D

Figure 4.3: The number of tigers (A) and the number of prey killed (B) as a function of T_{fol}, the number of dispersed tigers as a function of Ht_{rad}(C), and the number of prey as a function of G_m (D). Due to expensive computational costs, the repetition for each simulation were carried out for 15 times.

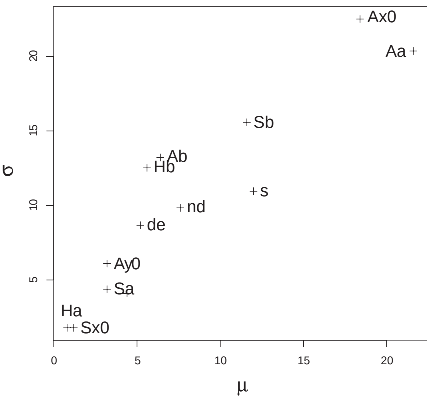


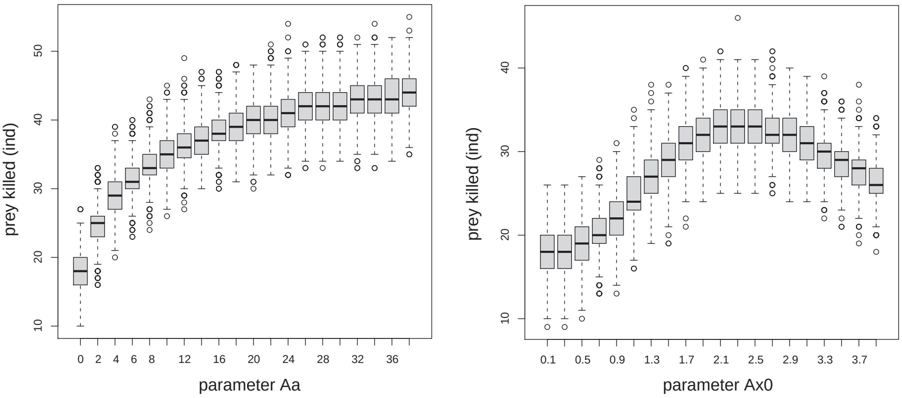
Figure 4.4: The plot of μ and δ values of all input parameters of the NFM model.

number of parameters were identified as having an intermediate influence on the prey killed compared to others. These were the parameters *Sb* and *Ab*, which are proportional to the range of prey sizes most (successfully) attacked, the size and number of prey items initially available (*s, nd*), the slope of handling time linear regression (*Hb*) and the predators encounter distance (*de*).

Similar to the PPP model, both *Aa* and *Ax0* were gradually changed to test their effect on the prey killed. Figure 4.5 shows the box plot diagram of the prey killed as a function of *Ax0* and *Aa* parameters. The non-parametric comparison tests showed a highly significant difference of number of daphnid eaten (Kruskal-Wallis, H= 28,540.51, $p < 0.01$) when the *Aa* were gradually changed over the values from 0 to 39. The number of prey killed was found to be sensitive between the values of 0 to 20, and relatively insensitive for the values above 20. The model output differed significantly when gradually increasing the parameter *Ax0* from 0.1 to 4.0 (Kruskal-Wallis, H= 9,319.57, $p < 0.01$) However, the number of prey killed by backswimmers did not show any similar sensitivities above or below certain values of *Ax0*: The model output was sensitive to the changes in parameter values from 0.5 to 1.9, and between the values of 2.6

Table 4.2: Description, range (minimum and maximum values for five larval instars (Gergs and Ratte, 2009)), units and relative importance of parameters of the NFM, based on μ and δ. Capital letters indicate the parameters of lognormal functions for calculating attack rates (ar) and success rates (sr) and the parameters of the linear function for calculating handling times (th). Small letters indicate ecological parameters.

Parameter	Description	Min	Max	Units	μ	δ
Aa	Parameter of ar, proportionality factor of max ar	5.4	11.2	-	21.6	20.37
Ax0	Parameter of ar, optimal s	0.7	2.06	mm	18.4	22.51
s	Prey size	0.6	3.7	mm	12.0	10.95
Sb	Parameter of sr, proportional to range of preferred s	-0.437	0,705	mm^2	11.6	15.58
nd	Initial number of daphnid prey	1	500		7.6	9.84
Ab	Parameter of ar, proportional to range of preferred s	0.16	0.4	mm^2	6.4	13.22
Hb	Parameter of th, intercept of linear regression	1.548	2.22	-	5.6	12.52
de	Encounter distance	0.508	2.02	cm	5.2	8.6
Sy0	Parameter of sr, proportional to minimum sr	-48.52	21	-	4.4	4.1
Ay0	Parameter of ar, proportional to minimum ar	0.4	3.2	-	3.2	6.1
Sa	Parameter of sr, proportionality factor of max sr	38.3	116.5	-	3.2	4.38
Sx0	Parameter of sr, optimal s	1.38	2.3	mm	1.2	1.79
Ha	Parameter of th, slope of linear regression	0.034	0.278	1/mm	0.8	1.8



A B

Figure 4.5: Prey killed as a function of parameter *Ax0* and parameter *Aa*. 1000 Monte-Carlo simulations were run for a three hours experiment with an initial prey density of 100/l. Simulations were run for the parameter set of 4th instar backswimmers foraging on a range of prey sizes (0.6 - 3.7 mm).

and 4. The numbers of prey eaten were shown to be relatively insensitive at values of *Ax0* between 2.0 to 2.5.

Comparing sensitivity-related to distances

The sensitivity of the number of prey killed as a function of the changing parameters of the hunting radius in the PPP model and encounter distance in the NFM were compared in order to gain an insight on the predator-prey system. Figure 4.6 A shows the prey killed by tigers fluctuated below the Ht_{rad} values of 400 meters and relatively insensitive to a change of hunting radius above that value (Mann Whitney U test, U= 5,199.50, p = 0.01). Figure 4.6 B displays a relatively high sensitivity of prey killed by backswimmers below a 2.0 cm of encounter distance, and relative insensitivity above that value (Mann Whitney U test, U= 2,469,448.50, $p < 0.01$).

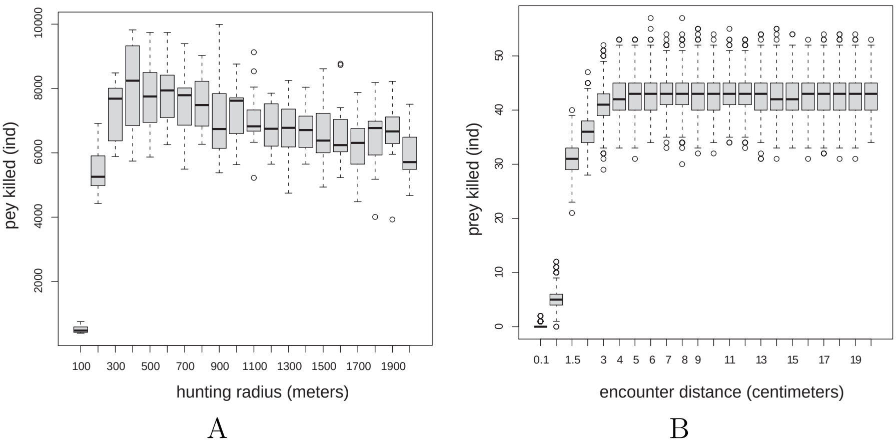


Figure 4.6: Boxplot diagram of the number of prey killed by tigers as a function of hunting radius in the PPP model (A) and the numbers of daphnid eaten by backswimmers as a function of attack distance in the NFM (B). Please consider that the x-axis has been extended for the lower values ($x < 2$) in the NFM model.

4.1.4 Discussion

The sensitivity analysis plays a major role in the development of ecological models in general (Thornton et al., 1979) and in population viability analysis, in particular (MacCarthy et al., 1995). Sensitivity analysis provides an insight into the interrelations between input parameters and output variables as well as into overall performance of the model, which is important for drawing conclusions from the data gained by simulations (Thornton et al., 1979).

In order to test the influence of parameters on the output of two individual based predator-prey models, this study successfully applied two methods for sensitivity analyses: an OAT screening technique referred to as the Morris method and gradually changing parameter values to test the effect on the model output. The latter method is usually applied for testing simple models or selected parameters only, which are considered important for the performance of a model (Hayes et al., 2000; Dechaume-Moncharmont et al., 2005; van Rijn et al., 2005). In the study presented, the Morris method turned out to be a feasible instrument for gaining a sound overview on the relative importance of model parameters, using reasonable computational efforts.

The sensitivity analyses of the PPP model have provided us with new insights into modeling processes for tiger-prey relationships. As carnivores, tigers are believed to depend on the prey abundance and size (Karanth and M.Stith, 1999; Miquelle et al., 1999a; Ramakrishnan et al., 1999; Karanth et al., 2004). Suprisingly, the number of tigers in the PPP model did not mainly depend on the density of the prey population as suggested by Karanth and M.Stith (1999) with the prey depletion model. The use of the homogenous spatial distribution between individual in the prey depletion concept has consequences on the dependency of the functional responses of predators on the prey density as indicated by Cosner et al. (1999). This might explain the dependency of the prey depletion model on the initial density of prey, but not for the PPP.

The number of tiger and prey killed in the PPP model are sensitive to the time required by tigresses to raise the cubs (T_{fol}). However, the outputs are very sensitive between T_{fol} of 670 to 680 days. The predator dynamics is known to be affected by the transition of immature predators into mature ones in an age stage structured predator population (Wang et al., 2006). In the PPP model, it is more likely the shorter the T_{fol}, the higher the number of tigers at the end of a simulation. A tigress is soon ready for the next reproductive periods after raising her cubs or being separated from them (Sunquist, 1981). The findings in this presented study disagree with Takahara's findings (Takahara, 2000) which considered a predator's individual needs to be the driver of the number of prey killed. In the PPP model, the predation behavior of a tigress with cubs is simulated differently to a tigress without cubs, as are sub-adult females and males as well as adult males. The hunger level of a tigress with cubs has higher increment than the other groups in every time-step than those groups. Thus, the longer the time invested for raising cubs, the more likely that prey will be killed by tigers as shown in the PPP model. The threshold, where the outputs were sensitive to a small change in the T_{fol}, agrees with the finding from Sunquist (1981) which showed an observation study at 660 days was used by adult female tigers to raise their cubs.

As revealed by the Morris method, the number of prey killed by backswimmers was highly influenced by the parameters *Ax0* and *Aa*, both of which are attack rate parameters in the NFM framework. The parameter *Ax0* equals the prey size which is preferentially attacked by a backswimmer instar. In laboratory studies it was shown that the prey size mostly eaten increases to some extent during the growth of the backswimmers (Gergs and Ratte, 2009; McArdle and J.H., 1979). For backswimmers of a particular size changing the value of *Ax0* led to an intermediate range of stabilized model output. In the sensitivity analysis, lower numbers of prey killed were observed below and above this range. The humped shaped pattern of the model output is in accordance with the prey sizes which are attacked most successfully, whereas capture success was found to decrease in smaller and larger prey for the instar shown (Gergs and Ratte, 2009). Thus decreasing or increasing *Ax0* in the analysis led to a lower number of prey items that were captured.

The parameter *Aa* influences the magnitude of the attack rate. Gradually increasing *Aa* directly leads to higher attack rates for a given prey size and thus to a higher total number of attacks. As can be expected from the characteristics of functional response curves of predators to prey density, the prey killed rose to a plateau when *Aa* was increased in the analysis. Similar to increasing prey densities in functional response curves the prey killed might be limited by the time spent on handling prey: The time predator and prey are exposed and the rate of attacks will influence the number of prey items killed. The time a predator spends on handling its prey will negatively influence the time available for searching and attacking prey (Holling, 1961). The sensitivity analysis revealed that values for *Aa* above 20 will not lead to significantly higher numbers of prey being killed. In actual fact, the range of values derived from direct observations appeared to be much lower than this threshold value (Table 4.2). In the study used for the model parameterisation, backswimmers were fed before being used in the experiments. Satiation minimizes the motivation of a predator to search for prey and thus reduces the rate of attacks (Hohberg and Traunspurger, 2009). Thus, higher attack rates can be expected from animals with increasing hunger levels.

The Morris method has proved to be a valuable tool for recognizing an unknown parameter (hunting radius) in the PPP model. In the PPP model, the number of dispersed tigers are highly influenced by the hunting radius of individuals. This agrees with findings on the lynx (Pe'er and Kramer-Schadt, 2008) and the Florida Panther (Cramer and Portier, 2001) in that their models highlighted the importance of individual perception in the landscape and the ability to detect other individuals. The perception constraint of a predator was also highlighted by Berec (2000) to invoke the local omniscience of predators. Two very different predator prey systems in terms of data availability were used in this study. Despite a large body size, the natural behaviour of the tiger is difficult to observe, whereas the backswimmer behaviour can be observed through laboratory experiments as shown by Gergs and Ratte (2009) and Gergs et al. (2010). In the backswimmer model, the result of the encounter distances from the simulation can be compared with experimental results. Thus a parameterization of this factor can be feasibly be cariied out. However, this parameter is difficult to measure in the field and almost imposible to carry out in some form of experimental situation for large carnivores such as tigers, panthers, lynx, etc. Therefore, further study on the distance at which carnivores can detect their prey will provide a valuable contribution to gain insight into predator-prey system through modeling or empirical studies.

This study has shown the use of the sensitivity analysis for deriving some possible general rules in predator-prey systems. By gradually changing the hunting radius in the PPP model and the encounter distance in the NFM, this study shows trends for regions where the number of prey killed are either sensitive or insensitive. Both models show a certain threshold at which the sensitive region turns into an insensitive one. It was recently shown that animal body masses might play a role in the utilisation of space (Jetz et al., 2004) and that encounter distance can be expressed as a function of insect larval stage (Gergs and Ratte, 2009). Furthermore, Kooijman (2000) suggested that life history traits such as the ingestion rate are generally proportional with the body size of an animal. Such studies might indicate possible relationships of scale between hunting distances and the body sizes of predators. For the parameterisation of individual-based predator prey models, further studies involving different taxonomic groups and predator-prey systems, are urgently needed to test this rule and to deduce general rules for extrapolation between species.

4.1.5 Conclusions

The role of sensitivity analysis in the development of ecological models has often been neglected. Moreover, expensive computational costs may have hindered a comprehensive analysis of complex individual-base models. In this study, the Morris method served as a feasible instrument for gaining a sound overview of the relative importance of model parameters, using reasonable computational efforts.

Factor screening should be recognized as an important step during the development of IBMs. Screening methods, accompanied by the simple technique of gradually changing parameter values, provide a useful tool for gaining insight into both complex and simple ecological models such as the PPP and the NFM.

4.2 Where to Go and How to Hide? Measuring the Relative Effect of Movement Decisions, Habitat Quality, and Landscape Configuration on the Mortality and Migration of Tigers' Prey

Muhammad Ali Imron, Sven Herzog, Uta Berger

Summary: The previous section showed that the outputs of the PPP model were sensitive to parental-care time duration, the hunting radius, and the growth rate of prey. Among these parameters, the hunting radius of tigers is relatively unknown. This section demonstrates the estimation and justification of the hunting-radius parameter through known tiger-prey relationships. This section also demonstrates the use of the PPP model to test the effect of movement decisions made by prey, habitat qualities, and landscape configuration on prey' mortality and migration.

This section is being prepared to be submitted in the Journal of Landscape Ecology and based on two conference papers: MatGeoS'09 Geosciences from Earth to Space, the 2nd International Workshop on Mathematical Geosciences, TU Freiberg, December 2009 (*http://www.iamg.tu-freiberg.de/assets/docs/pdf/matgeos09_proceedings.pdf*) and the Land-use Policies and Sustainable Development in Developing Countries (LUPIS) conference, Gadjah Mada University-Indonesia, November 2010 (*http://sites.google.com/site/regconference2010/*).

Abstract Prey depletion is one of the most important factors for determining the survival of tigers in the wild. Understanding the response of prey in the presence of different habitat qualities and landscape configuration under the pressure of predation is a challanging topic for tiger conservation. The Panthera Population Persistence (PPP) - a spatially explicit individual-based model for the Sumatran tiger, was modified to address the question whether the mortality of two different prey species and migration are affected by habitat qualities, landscape compositions, and the movement decisions of prey. Two types of prey mortality (natural mortality and tiger predation), and the emigration rate of prey were measured in five habitat qualities and four landscape compositions. To investigate whether movement behaviour adaptation results in prey depletion, three movement decisions- random movement, optimal movement, and species-specific movement- were tested against prey mortality. The simulation results showed that habitat quality affects the natural mortality and mortality due to predation in similar patterns, whereas the prey migration followed reverse patterns. These findings suggest that a good habitat quality allows prey to survive and thus available for tiger consumption. When a low habitat quality was combined with a high quality habitat, the number of migrating prey was high, reducing resources for the tigers. This indicates that landscape composition should be considered when predicting Sumatran tiger population persistence. Optimal-movement of two different prey species resulted in a high density of prey in high-quality habitats, providing highly concentrated prey densities in tiger habitats, but resulted in lower tiger predation rate than random movement and species specific movement. Validation of the model against existing studies on the consumption rate of tiger on prey indicates that the PPP model is confident enough to be used to assess three trophic interaction between habitat, prey, and tiger.

4.2.1 Introduction

The dependency of tigers on prey availability suggests that the depletion of prey populations is responsible for the decline of tiger populations (Ramakrishnan et al., 1999; Karanth et al., 2004; Sunquist et al., 1999). Tigers are able to persist in a very wide range of habitat conditions (Miquelle et al., 1999a; Sunquist, 2010). However, tigers are also known to have site fidelity and territoriality in order to successfully survive and reproduce (Miquelle et al., 1999a). High predation rates and reduction of high-quality habitats are the main causes of prey depletion (Sutherland, 1996; Fahrig, 2007b).

The tropical forest in Sumatra island has experienced severe consequences from development during the last two decades. The tropical forest on this island have been dramatically reduced and converted into other land-use types such as settlement, agriculture, palm oil plantation, etc (Gaveau et al., 2007; Linkie et al., 2003; Kinnaird et al., 2003; Uryu et al., 2007; Maddox et al., 2007). Hence, the landscape of Sumatra island consists of habitat with different qualities and compositions for tigers and their prey. In order to ensure population persistence, conservation strategies should consider the quality of the whole landscape (Fahrig, 2001). In the presence of a heterogenous landscapes as a result of human development, understanding the ability of a species to respond to various habitat quality in the landscape is important for predicting population persistence (Kareiva, 1987; Sutherland, 1996; Wiegand et al., 2005). Additionally, individual variations and behaviour can influence the dynamics of a population (Revilla and Wiegand, 2008). Thus, understanding the response of prey populations to different habitat types and composition should be understood on the individual level.

Habitat quality and composition play an important roles on the dynamics of metapopulations (Moilanen and Hanski, 1998). These two factors affect the risks and benefits from different cover types for certain species (Fahrig, 2007b; Russell et al., 2003; Nathan, 2008; Wiegand et al., 1999). In addition, small differences in movement behaviours greatly affect metapopulation dynamics (Hawkes, 2009). Studies showed that the densities of tigers and prey varied across different habitat types in Sumatra (Franklin et al., 1999; Linkie et al., 2003; O'Brien et al., 2003; Linkie et al., 2006; Hutajulu, 2007). However, these patterns could not provide insight into the response of individual prey to the presence of different habitats and landscape configurations. As carnivores live in a heterogenous landscape, understanding the population dynamics of the Sumatran tiger also requires insight into the effect of habitat qualities and configurations on the mortality of prey.

The main cause of the persistence of prey, is primarily a result of a change in predator prey preference, as they move onto other prey species in response to scarcity (Begon et al., 2006) and due to morphological and behavioural adaptations (Matter and Mannan, 2005). Behavioural adaptation of prey includes how the prey use specific habitat features which might reduce the probability of being killed by a predator. The behavioural adaptations in response to specific habitat features are sometimes represented by movement behaviour of individual implemented in a model. The movement decision at the individual level is known to affect the dynamics of a population (Kramer-Schadt et al., 2004; Cramer and Portier, 2001). In addition, movement rules have been recognized as critical features for determining the stabilization mechanisms in predator-prey systems (Hosseini, 2006). Thus, knowledge of prey's individual movement decisions will enhance our understanding about the persistence of prey mechanism in a heterogenous landscape.

Empirical studies investigating the relationship between Sumatran tigers and prey in different landscape configurations is an ideal approach for understanding the adaptation response of prey in different habitat qualities and landscape compositions. However, the high rate of habitat conversion in Sumatra has made this approach almost impossible to be implemented in the field. Therefore, an alternative approach should be used to overcome this problem. An individual-based model (IBM) approach can be used to simulate the behaviour of individuals and their interaction with other individuals and their environment, while at the same time, this approach enables an observation of the emergence at population level (Grimm and Railsback, 2005; Grimm et al., 2006). This present study demonstrates the use IBM as an alternative approach for understanding the mortality of prey populations under different rules of movement, habitat qualities, and landscape configurations.

4.2.2 Model Description

The model description follows the ODD (overview, design concepts and details) protocol for describing individual- and agent-based models (Grimm and Railsback, 2005; Grimm et al., 2006). The basic Panthera Population Persistence (PPP) model as explained in Chapter 3, was modified as follows:

Overview

Purpose The purposes of the modified PPP model is to investigate the effect of individual prey movement, habitat qualities, and landscape configuration on the migration rate and mortality of the Sumatran tiger's prey.

States variables and scales The PPP model comprises of three animal species, the Sumatran tiger (*Panthera tigris sumatrae*) and two of its prey species; the Sambar deer (*Rusa unicolor*) and the Red Muntjac (*Muntiacus muntjac*). The individuals of tigers have different sex and age classes, hunger and starvation levels, and reproductive-based state variables (See Chapter 3). Sambar deer and Red Muntjac have age and hunger levels. The Sambar deer represents large prey which is preferred by tigers but its population density is relatively low on Sumatra island (O'Brien et al., 2003). The Red Muntjac have a relatively high population density in Sumatra's tropical forest (O'Brien et al., 2003) and represents a common small prey species for the tiger. Table 4.3 illustrates the description of state variables for each species in the PPP model. The simulated area is 203 x 149 grid cells. Each grid cell represents 12.7 hectares and is specified by habitat quality as explained in the initialization and scenarios sections.

Process Overview and Scheduling

Ageing All individuals increase in age with a time-step of 0.5 days.

Table 4.3: Description and unit of state variables for individuals in the PPP model

Individuals	State variables	Description	Values and units
Prey	age	age of individuals	Sambar deer (0-6,120 days) (Nugen et al., 2001) Red Muntjac (0-3,600 days) (Chapman et al., 2005)
	hunger level	energy level of an individual	0 -200 (Adjusted parameter)
Sumatran tiger	hunger level	energy level of an individual	0-100 (Ahearn et al., 2001)
	starvation level	starvation level of individual	0-30 (Ahearn et al., 2001)

Prey Movement Prey movement is defined by two main factors: distance and direction. Distance refers to data obtained for Red deer movement which varies from 0.23 - 7 km/day (Fryxell et al., 2008). This variation covers both the encamped mode (more sedentary behaviour) and exploratory mode (rapid directional movement). The direction of prey movement is determined by random direction with persistence (Ahearn et al., 2001). The direction of movement has a higher probability of follow previous direction of movement. Figure 4.7 ilustrates the concept of movement direction of an individual of prey. The decision whether a prey will move or stay in the current grid cell is determined by habitat quality of current, in comparison with that of the neighbouring grid cell. The probability of decision to move is calculated as follows:

$$\alpha = \beta 1/(\beta 1 + \beta 0) \tag{4.1}$$

with α being the probability of decision to move to the next patch, $\beta 1$ representing the habitat index of the next path and $\beta 0$ denoting the habitat index of the current patch. Three movement decision of prey are explained in the section Scenario and Analysis.

Foraging behaviour of prey The foraging behaviour of prey is driven by hunger level of individual prey. Each individual increases its hunger

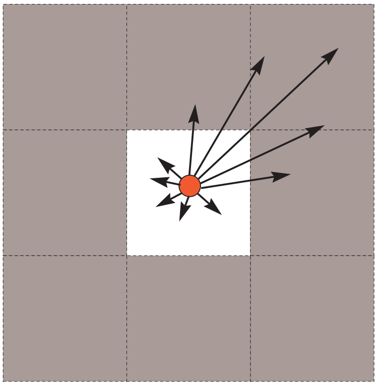


Figure 4.7: Movement direction of individual in the PPP model follows random direction with persistence. The white box represents the current grid cell occupied, and grey boxes represent neighbouring grid cells. The vectors represent the probability of the movement direction. The longer the vector, the higher the probability to move in the same direction (adapted from Ahearn et al. (2001)).

level 10 levels per time-step. The foraging activity of prey results in the reduction of hunger level by the value of the habitat quality of the grid cell where it located per time step.

Reproduction The PPP model did not specify sex of prey, thus reproduction of prey was simulated as follows. Red Muntjac starts to reproduce annually from the age of 2 to 4 years and the number of litters varies from 0 to 3 individuals. Sambar deer annually reproduce with a random probability of 0 or 1 individuals starting from 2 to 6 years. Both Sambar and Red Muntjac have density-dependent birth rates. Both will continue to reproduce until the population reaches the carrying capacity. The carrying capacities for both prey species is based on the maximum density in the Sumatran tropical forest (O'Brien et al., 2003). The carrying capacity of Sambar deer in the PPP model is 1.4 ind/km^2 and Red Muntjac is 4.4 ind/km^2.

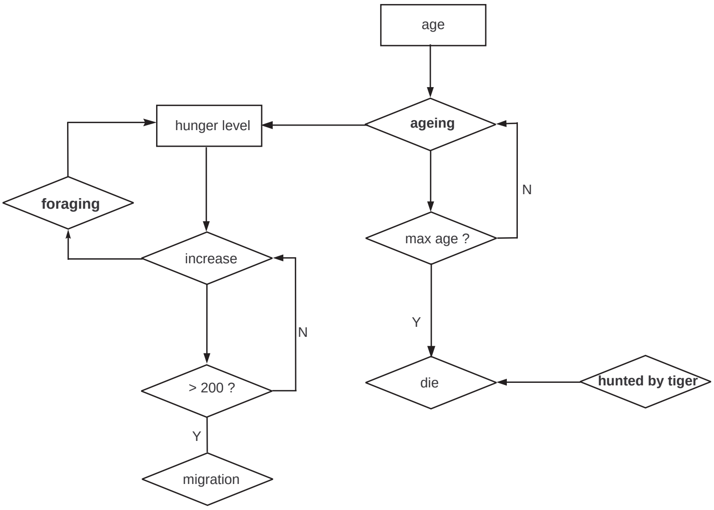


Figure 4.8: Basic procedure of prey behaviours determining death of individual of prey due to natural cause or by tiger, and migration behaviour due to starvation. The bold letters indicate sub-models explained in the model description.

Mortality Prey dies due to two factors, reaching a maximum age and death caused by tiger. The maximum age is approximately 17 years and 10 years for Sambar deer and Red Muntjac, respectively. Hunting behaviour exhibited by tigers lead to prey death. Figure 4.8 depicts the processes of determining the death of individual prey from both natural causes and those killed by tigers.

Migration The PPP model simulates the migration of prey to other areas in relation to foraging behaviour. If a prey could not balance the hunger level with foraging behaviour in the present habitat, a prey will experience starvation (the hunger level exceeds 200) and will be removed from the system as migrating individuals.

Design Concept

Emergence The population dynamics of two prey populations are expected to emerge as results from individual interaction between prey-habitat, prey-tiger, and ageing behaviour.

Interaction Interaction in the PPP model exists between prey-habitat as well as between tiger-prey. The prey-habitat interaction is demonstrated by both the movement behaviour of prey and foraging behaviour. The tiger-prey interaction is described by the hunting and feeding behaviour of the tiger.

Adaptation Movement decision of prey is the mechanism of prey adaptation in different landscape configurations and explained in the scenario and analysis sections. The PPP model assumes that the movement of prey is not affected by the presence of tigers in the landscape, thus there is no tiger avoidance behaviour by prey.

Sensing A prey senses its own age and hunger levels which determine the behaviour corresponding to these two factors. Prey can also sense the habitat quality of its current grid cell and the neighbouring grid cell to be considered in the movement behaviour. However, in the PPP model, a prey cannot sense the presence of tigers, thus prey movement is independent from that of tigers.

Stochasticity The stochasticity is set to the probability of an individual to move to the next patch and the probability of the number of infants produced by prey.

Collectiveness Individual prey do not adhere to collectiveness as a result of interaction with other individuals.

Details

Sub-models In the PPP model, tiger behaviours are simulated by considering internal and external conditions. However, this study will only incorporate predation behaviour of tigers, hunger, starvation, hunting, and feeding, which is important factor for the prey population. The predation behaviour of tiger starts with hunger and starvation behaviours. Tigers have hunger levels from 0-100. In each time step the hunger level increases 10 levels and when it reaches 60, the tiger starts to hunt. Tiger searches for prey in a hunting radius and has a preference for Sambar deer. If there are no Sambar deer available within its hunting-radius, tigers will feed on Red Muntjac. Tiger feeding is not interrupted if it occurs in a high-quality habitat, but is interrupted when it occurs in lower-quality habitat, as illustrated in the empirical study (Kerley et al., 2002). The feeding behaviour of tiger reduces the hunger level by 12 per time step. However, if a tiger reaches a hunger level higher than 90, tigers will experience starving, and continued starvation for more than 30 days will cause death. Adult and sub-adult tigers exhibit spatial arrangement. Adult tigers display territorial behaviour (Franklin et al., 1999). Since sub-adults do not have any home range, this age class performs territory establishment by considering the distance from other individuals.

Initialization The density of prey population were set according to existing prey density studies on the Sumatran tropical forest (O'Brien et al., 2003). The Red Muntjac density was set at 3.96 ind/km^2, while Sambar deer was fixed to 0.88 ind /km^2. Both prey species are randomly distributed in the space. Twenty individuals of tigers, consisting of 10 sub-adult males and 10 sub-adult females were distributed randomly in the space.

Implementation The PPP model is implemented in NETLOGO v. 4.1. (Wilensky, 1999). Each scenario was carried out for a simulation time of 365 time-steps with 30 repetitions.

Scenarios and Analysis

To test the effect of habitat qualities and landscape composition, nine scenarios consisting of five homogeneous habitats and four combined habitats were tested. The homogeneous habitat scenarios consist of different habitat qualities ranging from the best quality (E), to high (D), medium (C), low (B) and the lowest (A). The landscape configuration scenarios are a combination of the best habitat qualities with lower habitat qualities. The configuration between the best habitat quality and the lowest quality is denoted as F, with low quality (G), medium quality (H) and high quality (I). Additional habitat quality was included to represent habitat edge. Edge habitat is 5 grid cells from the border between high habitat quality and low habitat quality, towards the direction of centre of high habitat quality. The habitat quality of edge habitats is calculated as average value from the sum of the highest and its surrounding habitat qualities. Figure 4.9 shows the initialisation of the PPP model in different habitat qualities and landscape compositions.

This study also tested three types of prey movement decisions: random movement, optimum movement, and species-specific movement. Regardless of the value of movement probability (α), within the random-movement framework, all prey individual will move to the next grid cell. This means that the habitat quality is not an issue for this type of movement decision. Within the optimum movement framework, both Sambar deer and Red Muntjac only move to neighbouring cells that have an equal or higher habitat quality than its current grid cell. The species-specific movement assumes that Sambar deer and Red Muntjac exhibit different types of movement. This is based on the findings that body size of quadrupedal animals can be used to explain the type and ability of their movement (McMahon, 1975). Within the species-specific framework, the movement of the Sambar deer follows optimum movement, whereas Red Muntjac movement follows random movement. Tiger movement follows the optimum-movement rules.

Data collected in each simulations represent number of individual of prey that die due to natural causes, prey killed, and the number of prey migrating from the system. Prey death from natural causes was determined by number of prey die due to maximum age. Prey killed is number of

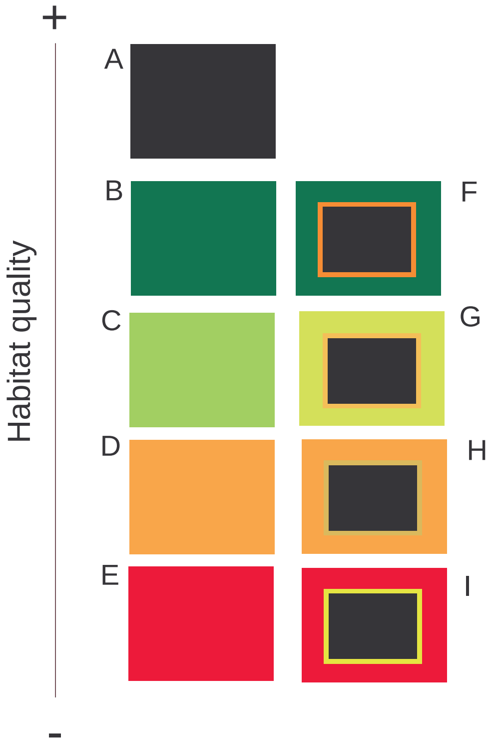


Figure 4.9: Landscape composition of the PPP model with different habitat qualities (a-e) and landscape compositions (f-i). Each colour represents different habitat-quality values. The landscape compositions consist of the highest habitat quality in the centre of the landscape(black), surrounded by a lower habitat quality, and an average habitat quality (border) between the highest and surrounding habitat.

prey predated by tigers. Migrating prey was calculated from the number of prey which experiencing accute starvation and then leaving the system. Non-parametric comparison using the Krusskal-Wallis and Mann-Whitney U tests were carried out using SPSS Version 11 for comparing the results from different habitat qualities, landscape compositions, and movement decisions.

4.2.3 Results

Model Validation

The predation rate per tiger, as indicated in existing literature, is used to validate the performance of the inter-relationship between tiger and prey. The individual consumption rate of tigers on prey was estimated to be between 5-6 kg of meat/day (Sunquist, 1981), resulting in 1825-2190 kg of meat/year (Sunquist et al., 1999). Results from simulation in the PPP model showed that within 6 months, a tiger consumes an average of 7.70 Red Muntjac individuals and 8.76 Sambar deer individuals. If a Red muntjac is assumed to be 20 kg and Sambar deer is 150 kg (Sunquist et al., 1999), in total a tiger in the PPP model consumed 2660.4 kg/year. As the entire body is not eaten (prey are approximately 30% inedible), the total consumption of prey per individual is 1862.28 kg/years. This values is within the range defined by existing tiger literature.

Prey Death from Natural Causes

In general, numbers of both prey species death due to natural causes was significantly different across different habitat types (Krusskal-Wallis ; H= 114.67 $p < 0.01$). The Mann-Whitney U test also illustrated that the number of prey deaths from natural causes differs significantly between lowest, low, and medium quality habitats. However, the medium, high, and highest quality habitats did not show any significant difference. The number of prey death showed a sensitive region between habitat quality from low to medium habitats quality, as illustrated in Figure 4.10. Prey death from natural causes also showed a significant difference among landscape configurations (Krusskal-Wallis ; H= 114.57 $p < 0.01$). The Mann-Whitney

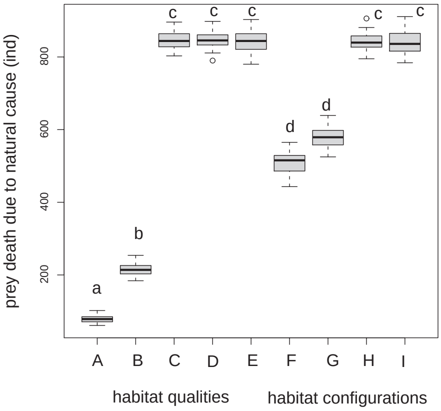


Figure 4.10: Numbers of prey (Sambar deer and Red Muntjac) deaths due to natural mortality in different habitat qualities (A-E) and habitat configuration (F-I). Small letters indicate significant difference at < 0.01 using the Mann-Whitney U Test.

U test among landscape configuration scenarios showed that scenario F and G were not significantly different, but they were significantly different from scenario H and I. The virtual landscape configuration showed that if the best habitat quality is combined with low-quality habitats, the natural mortality of prey were lower than those with a combination of medium to high habitat qualities (Figure 4.10).

Killed Prey

The number of both of prey species killed by tigers showed similar pattern as number of prey death due to natural causes. The number of prey killed by tiger is significantly different across all habitat qualities (Krusskal-Wallis ; H= 114.70, $p < 0.01$). The Mann-whitney U test showed that the number of prey killed is significantly different between the lowest (A) and low (B) habitat qualities. These two habitat qualities also show a significant different from medium- high- and highest-quality habitats. Figure 4.12 shows that the number of prey killed by tigers is sensitive from low habitat quality (B) to medium habitat quality (C). The habitat config-

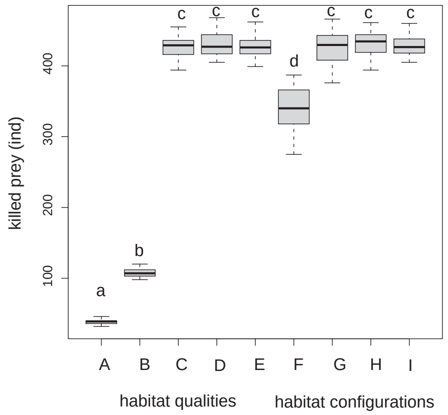


Figure 4.11: Numbers of prey (Sambar deer and Red Muntjac) killed by tiger in different habitat qualities (A-E) and habitat configuration (F-I). Small letters indicate significant different at < 0.01 using Mann-Whitney U Test.

uration scenarios also showed a significant difference for the number of both prey species killed by tigers (Krusskal-Wallis ; H= 66.70 $p < 0.01$). However, only scenario F showed a significant difference from all other scenarios for landscape configruation. In addition, the number of prey killed was sensitive between landscape scenario F and G as seen in Figure 4.12.

Prey Migration

The number of both prey species migrating due to starvation is significantly different across all habitat type scenarios (Krusskal-Wallis ; H= 144.33, $p < 0.01$). However, the pattern of difference is reverse from the number of deaths caused by natural causes and tigers (figure 4.12). The Mann-Whitney U test resulted in an insignificant difference in the number of prey migrating in the lowest and lower habitat qualities, but these two types of habitats were significantly higher than medium- high- and the highest-quality habitats (figure 4.12). However, the number of migrating prey is sensitive between low habitat quality to medium habitat quality. The number of migrating prey is also significantly different between landscape configuration (Krusskal-Wallis ; H= 111.49 $p < 0.01$).

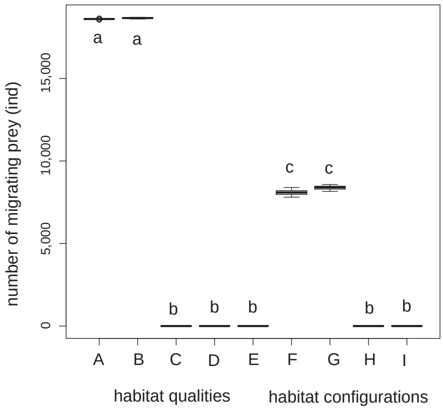


Figure 4.12: Numbers of prey (Sambar deer and Red Muntjac) migrating due to starvation in different habitat qualities (A-E) and habitat configuration (F-I). Small letters indicate significant difference at < 0.01 using Mann-Whitney U Test.

Mann-Whitney U test showed an insignificant difference in the number of migrating prey between landscape configuration F and G, but these two landscape configurations were significantly higher than landscape configuration H and I (figure 4.12). Similar to habitat quality, the number of migrating prey is sensitive between scenarios of the best habitat quality combined with low habitat quality and scenarios where the best habitat quality was combined with medium habitat quality .

Effect of Movement Decisions

The individual distribution in the landscape as a result of different movement decisions are shown in Figure 4.13. Both Sambar deer and Red Muntjac are concentrated in the highest habitat quality for all types of movement. However, both prey species also foraged in nearby lower habitat qualities if random movement was used. The distribution of both prey species are limited to high and medium habitat qualities when optimum-movement was used. The distribution of Sambar deer was limited to the high and medium habitat quality, but Red Muntjac was able to forage in nearby grid cells with lower habitat quality when species-specific movement was applied.

The three prey movements affect prey mortality and migration in different patterns as seen in Figure 4.14. A significant difference in the number of prey deaths due to natural causes (Krusskal-Wallis ; H= 60.73, $p < 0.01$) was found and the Mann-Whitney U test showed that optimum movement is the highest among other types of movement. The number of killed prey also showed a distinct difference between movement rules (Krusskal-Wallis ; H= 26.52, $p < 0.01$). However, the pattern was reverse from that of prey death due to natural causes. The Mann-Whitney U test of number on the prey killed by tigers is the lowest among the two movement types. The number of migrating prey in optimum movement was the lowest (figure 4.14) and illustrates clear separation from other movement types (Krusskal-Wallis ; H= 79.12, $p < 0.01$).

4.2.4 Discussion

Simulation results showed a general tendency; number of prey death due to natural causes and predation in higher habitat qualities are higher than in low habitat qualities. Habitat qualities affect the amount of energy consumed by prey which also leads prey to migrate due to starvation. When prey occupy low habitat qualities, the probability of prey leaving the system due to migration is high because prey could not fulfill their energy requirement. When the number of prey migrating from the system is high, the density of remaining prey is lower, and thus the probability of being killed by tigers is also lower. As a consequence of a high rate of migration, the number of prey dead from ageing is also lower because the high migration rate reduces individuals which would potentially experience death due to old age. However, the two types of prey mortality and migration are highly sensitive to the habitat quality. This suggests that further study on foraging behaviour of both Sambar deer and Red Muntjac in different habitat qualities is important for enhancing the performance of the PPP model.

The simulation results showed that the naturally caused mortality and predation mortality performed in a similar pattern due to the effect of habitat configuration. The lower the habitat quality surrounding the highest habi-

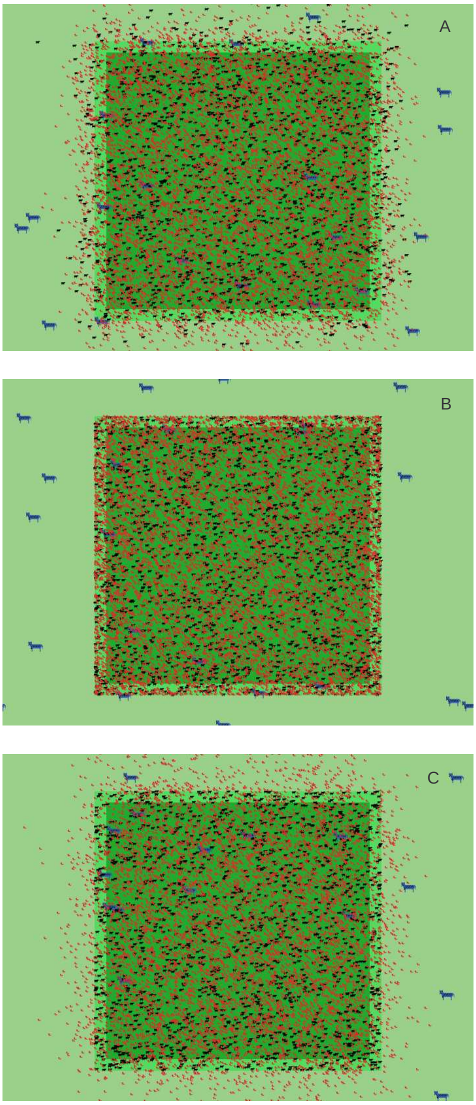


Figure 4.13: Visualisation of the effect of prey movement decisions on individual distribution of prey using the same landscape configuration. The Sambar deer is symbolized by the black dot, the Red Muntjac is the red dot, and tiger is represented by blue. (A) is the random-movement decision, (B) is the optimum-movement decision, and (C) is the species-specific movement decision.

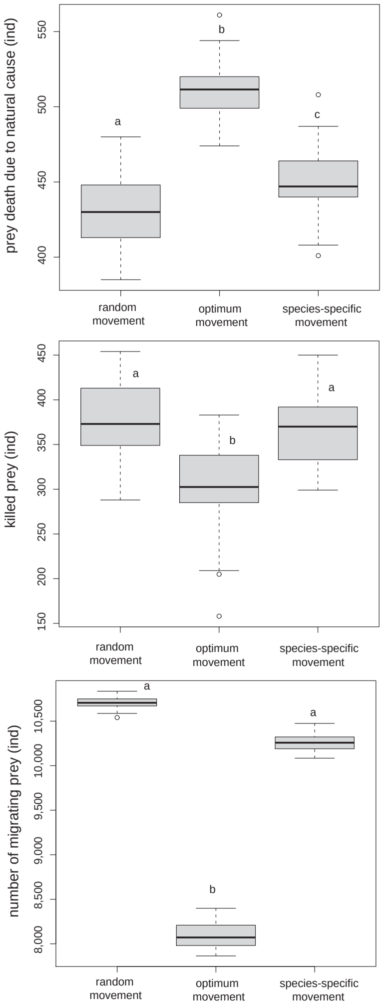


Figure 4.14: Number of prey deaths due to natural causes, those killed by tiger, and migrating prey in the same landscape configuration. Small letters indicate significant difference at < 0.01 using Mann-Whitney U Test.

tat quality, the lower the number of prey deaths due to natural mortality and tigers. The higher the number of prey the higher the probability of migration due to starvation. Conversely, when the best habitat quality is surrounded by slightly lower habitat quality, the number of prey migration is lower and thus the number of prey death from natural causes and predation is high. The landscape configuration in this study only covered three different habitat qualities. The two habitat types represent the highest habitat quality and the lowest in each landscape configuration. Each of these two habitat qualities covered almost the half size of the landscape. The habitat quality of the third type is the average between the lowest and highest habitat quality in the landscape. This third habitat quality represents the smallest habitat size among the other two habitats. The configurations as seen in the landscape configuration scenarios, represent virtual situations in a protected area and its surrounding landscape. The protected area has the highest habitat quality, while the surrounding landscape has the lowest. The third habitat quality represents the edge, which plays an important role for wildlife population (Woodroffe and Ginsberg, 1998), and particularly for tigers (O'Brien et al., 2003). Evaluation on the size and quality of the edge will provide insight into the effect of edge for the survival of tiger and its prey.

The individual movement behaviour provides a great contribution to the understanding of the causes and consequences of the individual behaviors for spatial dynamics of populations (Schick et al., 2008). Movement rules have been recognized as critical features for determining the stabilization mechanisms in predator-prey systems (Hosseini, 2006). The results from this study show that optimal movement performed differently than random and species-specific movement. The mortality of prey due to natural causes was at its highest when prey move in optimum manner. When prey move in the optimum way, the prey will have a higher probability to survive due to its ability to sense and move to a similar or higher-quality habitat. Prey mortality using optimum movement showed that natural mortality contributes higher than mortality from predation. This indicates that tigers consume less prey if prey and tiger move in the same optimum manner. The feeding behaviour of tigers explain the lower number of prey killed in optimum movement. Since hunting and feeding only occur in high-quality habitat, tigers maximize the time to feed, resulting in a lower number of prey killed. Thus, tigers optimize their searching time for hunting and follow functional responses of predators (Holling, 1959). In contrast, when prey is able to move to lower-quality habitat, the killing and feeding by tigers may occurr in this low habitat types. Tigers spend less time consuming prey when kills are made in human-affected areas, while in undisturbed areas tigers are more likely to eat more meat and spend more time doing so (Kerley et al., 2002). In lower-quality habitats, tiger feeding behaviour is not maximum, hunger level of tiger is not maximally depressed, and these conditions initiate the next hunting occasion. Consequently, the tiger will hunt more prey.

The density of individuals per patch has been found to be higher when individuals move in optimum rather than random movement (Russell et al., 2003). The findings in this study confirm that optimum movement of prey limits the distribution of prey in the landscape, and thus higher prey density emerged in high-quality habitats. However, as the PPP model did not simulate intra- and inter-specific competition, such as the effect of prey densities on a patch and kin competition avoidance, these factors might affect prey distribution in the landscape (Fahrig, 2007b). Additionally, the PPP model assumes that the presence of tigers does not affect the distribution of prey population and prey does not have any behavioural response for these situations. The evaluation of the effects of these factors on tiger searching time during hunting behaviour will enhance understanding of the predator-prey interaction in heterogenous landscapes.

The predator population dynamics are affected by individual movement decision, as found in lynx (Kramer-Schadt et al., 2004) and Florida panthers (Cramer and Portier, 2001). This suggests that similar mechanism can also be occur in the Sumatran tiger. Therefore, further studies about movement responses of the Sumatran tiger to the presence of heterogenous landscape should be carried out to complement existing studies. However, particular attention should be provided to the ability of each species to percieve habitat barrier and qualities in the landscape, such as the presence of riverine area as habitat for wild boar (Choquenot and Ruscoe, 2003) and main roads and human densities for Sumatran tiger (O'Brien et al., 2003; Kerley et al., 2002). These factors can be represented by a raster-base or vector-base maps (Tischendorf, 1997) and might result in different consequences for the population dynamics (Fahrig, 2007b).

4.2.5 Conclusions

The PPP model successfully simulated the impact of different habitat qualities, landscape configurations, and movement decisions on two main causal factors for prey mortality and migration due to starvation. The individual traits and behaviour of two different prey species had distinct consequences at the population level due to different habitat quality and landscape composition. The patterns from the investigation of habitat qualities clearly show that the number of migrating prey was higher in low habitat qualities, affecting the prey available for tigers. If a high habitat quality, such as a protected area, is composed with low habitat quality, the landscape composition could not support prey to survive and would result in high-level prey migration. Optimal movement of two different prey resulted in a high density of prey in high-quality habitats, providing a concentration of prey in tiger habitats, illustrated a lower predation rate for tigers than random and species-specific movement. The validation of the model with currently available studies on the rate of prey consumption by tigers have shown that the PPP model is confident enough to be used to assess three trophic interactions between habitat, prey, and tiger.

4.3 The Extinction Potential of a Sumatran Tiger Population after the Removal of Poaching

Muhammad Ali Imron, Sven Herzog, Uta Berger

Summary: The previous section demonstrated one part of the model analysis by testing the effect of habitat quality, landscape configurations and movement decisions on prey mortality and migration. This section demonstrates the use of the PPP model for practical conservation of the Sumatran tiger population by testing the effect of tiger poaching, prey depletion, and a combination of both on the extinction probability of a Sumatran tigers population. This section also depicts the use of the PPP model to answer whether anti-poaching programs are effectively reducing the probability of extinction on the 20-year time horizon.

This section is being prepared for submission to *the Journal of Animal Conservation.* An earlier version was presented at the 6^{th} International Tropical Zoology Conference, Bonn, May 3-8, 2009.

Abstract Tiger poaching and prey depletion are among the most important factors for determining the persistence of tigers in the wild. These factors may occur simultaneously and imperil the remaining tiger population. To deal with these situations, anti-poaching programs have been deployed to disarm traps in protected areas. The PPP model was modified for testing the probability of extinction of tigers in the presence of tiger poaching, prey poaching, and a combination of both. The model was also used to investigate the probability of extinction after the removal of poaching by anti-poaching programs. Comparison of the probability of extinction from three type of traps (tiger traps, prey traps, and multi-animal traps), trap densities, trap duration, and trap frequency were carried out. Additionally, this study also measures the "survival-threshold" which is an opposite point of view than looking for probability of extinction. The results showed that tiger-trap type has a stronger effect than other trap types. Among trap parameters, the magnitude of trap frequency is stronger than trap duration and density. Anti-poaching units were not able to reduce the probability of extinction if tiger poaching had previously occurred at a high density, duration, and frequency. However, anti-poaching units reduced extinction probability if prey and multi-animal trap had occurred at a high density, duration, and frequency. This study recommends improving the ability of anti-poaching units to detect the presence of poaching and to set out recommendations for the action of the units employ soon after poaching has been detected.

4.3.1 Introduction

Continued debates about the importance of tiger poaching and prey depletion has led to two mainstream paradigms for tiger conservation (Chapron et al., 2008). Since prey plays an important role for tiger populations, the prey depletion paradigm suggests that one tiger conservation priorities is to protect, maintain, and increase prey populations through multiple means, such as expanding habitats (Sunquist et al., 1999; Seindensticker et al., 1999; Miquelle et al., 1999a; Wegge et al., 2009; Steinmetz et al., 2010). The tiger poaching paradigm emphasizes the importance of poaching in tiger mortality in the wild. Poaching has been highlighted as one of major causal factors leading to a decline in tiger population in the wild

(O'Brien et al., 2003). Poaching explains the recent rapid decline in tiger populations as a result of increasing demand for products created from tiger parts (Dinerstein et al., 2007; Shepherd and Magnus, 2004). Therefore, reducing the numbers of poachers through the use of surveillance is an important approach for tiger conservation (Linkie et al., 2003; Kenney et al., 1995).

Surprisingly, recent findings on the rate of tiger poaching showed that the number of poached animal in core areas of national parks represented 58% of the total tigers poached, higher than in other protected area categories such as protected forests or wildlife reserves (Tilson et al., 2010). The findings highlighted that protected areas are not secure enough for protecting tiger populations in the wild from poaching. In addition, poaching in tiger habitats not only targets tigers, but also its prey (Linkie et al., 2003; Steinmetz et al., 2010; van Strien, 2006). Hence, poaching also potentially plays a role in prey depletion. The existing prey depletion and tiger poaching paradigms potentially overlook the fatal consequences of the presence of a combination of both tiger poaching and prey depletion for tiger conservation in the wild.

Anti-poaching programs have been deployed in the field to reduce the effect of poaching on both tigers and prey. The fact that population recovery has been recorded for the Amur tiger (Galster and Eliot, 1999) and prey population (Steinmetz et al., 2010) after the application of anti-poaching programs, has motivated similar program for the Sumatran tiger population (van Strien, 2006; Linkie et al., 2003). However, a long-term analysis has not been completed to measure possible population extinction after the removal of poaching. As the majority of Sumatran tiger populations are small and fragmented, population recovery after anti-poaching programs may not achieve its goal of population recovery, due to environmental and demographic stochasticity (Schrott et al., 2005). This may also be true for cases of anti-poaching program in tiger conservation. An effective conservation measure should understand the magnitude of the effect of important factors on population persistence (Fahrig, 2001). Hence, an understanding about potential of extinction after the removal of tiger and prey poaching pressures will enhance our ability to develop a sound conservation program for the Sumatran tiger.

The Sumatran tiger is categorized as a critically endangered species by the International Organization for Conservation of the Nature (IUCN, 2010) and recent population estimates predict that only 300 individuals remain in the wild. The cryptic character of this sub-species of tiger has made observations about its behaviour difficult to carry out in the field. Furthermore, poaching is an illegal activity. Thus to conduct an experiment about the effect of poaching on this tiger population is almost impossible. One of alternative approaches that could be employed to understand the effect of poaching on the persistence of tiger populations is individual-based modelling.

The first attempt to use modelling to test the effect of tiger poaching was carried out by Kenney et al. (1995), and were followed by O'Brien et al. (2003), and Chapron et al. (2008). The effect of prey depletion was modeled through a stage-based population model (Karanth and M.Stith, 1999) and inferences from field studies (Miquelle et al., 1999a; Ramakrishnan et al., 1999; Karanth et al., 2004, 2006). However, none of these studies tested the effect of the combination of tiger poaching and prey depletion. The most common approach for incorporating poaching and prey depletion involved simple matemathic calculations for mortality rates caused by poaching or prey depletion (Chapron et al., 2008; Karanth and M.Stith, 1999). However, this approach neglected environmental variations which required complex mathematical solutions (Chapron et al., 2008) and did not consider individual variations. As a population is composed of discrete individuals which have distinct traits and behaviour (DeAngelis and Mooij, 2005), it is therefore important to consider the magnitude of poaching on the persistence of tiger populations, especially response behaviour at the individual level.

An individual-based model (IBM) provides an effective way to evaluate different scenarios and hypotheses using all available knowledge about the system manifested in characteristic, quantitative and qualitative patterns, and can be used for practical conservation (Grimm, 1999; Grimm et al., 2006). IBM has been used for tiger conservation to support the tiger poaching paradigm (Kenney et al., 1995) and to investigate the effect of human-tiger conflict (Ahearn et al., 2001). The existing tiger poaching model, constructed by Kenney et al. (1995), only considered female sex class to determine the tiger extinction. This approach lacked the understanding of a possible "quasi-extinction" process, where extinction can occurr when one sex class is absent (Grimm and Wissel, 2004). The TIGMOD model by Ahearn et al. (2001) included almost all of the most important individual tiger behaviours and was simulated using a one-year time horizon. The TIGMOD simulated interaction between tigers and prey in a spatially explicit way. However, the interaction between prey and habitat was not simulated. Understanding the response of the predator population to landscape configuration should involve a three-trophic relationship of habitat-prey-predator (Ryall and Fahrig, 2006; Baeza and Estades, 2010).

This study demonstrates the modification of the Panthera Population Persistence (PPP), an individual-based model for testing the effect of tiger poaching, prey depletion, and a combination of both, and also poaching removal for the persistence of a Sumatran tiger population. The PPP model includes all important individual tiger traits and behaviours, including the three trophic interaction between predator-prey-habitat, as well as human effects created by poaching.

4.3.2 Model Description

The model description follows the ODD (overview, design concepts and details) protocol for describing individual- and agent-based models (Grimm and Railsback, 2005; Grimm et al., 2006). The Panthera Population Persistence (PPP) model was modified as per the purpose of this study.

Purpose

The purpose of the model is to assess the potential effect of tiger poaching, prey depletion, and their combination, a long with anti-poaching programs, on the extinction probability of a Sumatran tiger population.

State variables and Scale

This modified version introduced traps and anti-poaching units (APU) to represent poaching and poaching elimination programs, respectively. Traps

Table 4.4: Parameter description and units for traps and the anti-poaching unit in the PPP model

Parameter	Description	Units
Traps		
types	types of traps	no trap tiger traps prey traps multi-animal traps
density	density of traps	0.01 trap/km^2 0.05 traps/km^2 0.06 traps/km^2 0.07 traps/km^2 0.1 traps/km^2
duration	duration of trap stay in the system	short (1 week) medium (2 week) long (1 month)
frequency	interval to introduce traps into the system	1 year 6 months 3 months 1 month
Anti-poaching unit (APU)		
time-gap	time duration between traps introduced and removed from the system	no operation 1 week 2 weeks 1 month 6 months 1 year

have four parameters (*type, density, duration*, and *"frequency"*) and APU only has a time-gap parameter. Table 4.4 describes the parameters and units of traps and APU in the current PPP model.

4.3.3 Process overview and scheduling

The basic PPP model was simulated during the first year to let the model stabilize, free from the effect of the initiations. Poaching was ignited after one year by introducing traps into the system. The distribution of traps was random in the space, and with only one trap per grid cell. Tiger and prey traps are only able to catch tigers or prey, respectively. The multi-animal trap is able to catch both tiger and prey. Data about the probability of successful traping was difficult to uncover. The probability of successful trapping was assigned to be 50%. Traps stay in the system according to the trap *duration*. A trap will be removed from the system if it successfully catches an animal or after a certain time duration for each trap. The *frequency* of traps triggered the intensity of trapping that was present in the model. For example, a low *frequency* of trapping indicated that the trap will be inserted into the model every 6 months.

Anti-poaching units were deployed in the system according to the *time-gap* which is set in the model. The presence of anti-poaching units stopped the introduction of traps into the system and all trapping activities; if any traps were present in the model at the onset of the anti-poaching unit, the trap was unable to catch animals, becoming inactive.

4.3.4 Design

Sensing Traps are able to detect the presence of targeted individuals in the same grid cell.

Interaction The interaction between traps and animals is simulated in a spatially explicit manner. An animal is trapped with a 50% probability, if it steps into the same grid cell as the traps. Since the PPP model simulates the interaction between tigresses with cubs, if a tigress is poached, the cubs are also removed/die. If a tigress losses all her cubs due to poaching, the tigress is soon ready for the next reproductive period (Sunquist, 1981). If an adult individual with a home-range is trapped and removed from the system, the empty homerange will be occupied by any sub-adult or adult individuals without a homerange; this tiger subsequently establishes home range there.

Stochasticity The stochasticity is simulated for the succesful probability of traps to catch the target animal.

Observation The model is simulated using a 20-year time horizon for testing the effect of poaching on the probability of extinction of tigers with 30 repetitions. The number of individuals tiger remaining at the end of a simulation were counted to define whether a simulation resulted in absolute or quasi-extinction. Absolute extinction occurs when all tiger individuals (both male and female) are absent from the model. Quasi-extinction is the loss of one of the sex classes from the model due to mortality or dispersal. For each simulation, extinction is classified as either type, for further applications.

4.3.5 Scenario and Analysis

To investigate the magnitude of different trap parameters, one-factor-at-a-time (OAT) sensitivity analyses (Saltelli et al., 2004) were carried out. The experiments were carried out by gradually changing the *density, duration*, and *frequency* for each trap type. If a factor was being tested, the other parameters were set at medium values.

To find a 100% probability of extinction for all trap types, an additional three "extreme scenarios" were tested. The first set the density, duration and frequency to its lowest value, while the second was set to medium values, and the third to the highest values. The worst scenario for each trap type was then used to test the effectiveness of the anti-poaching unit to reduce the probability of extinction. As anti-poaching units only have time-gap parameter, the experiment only consisted of six experiments, using the time gaps as seen in Table 4.4. Only the worst scenario, that which resulted in 100% probability of extinction was considered for the anti-poaching unit test. During 20 years of model simulations, the number of runs which resulted in absolute or quasi-extinction are proportionalized to the total number of simulations.

This study introduces a threshold where survival might occur; the "*survival threshold*" ($P_S thresh$). The definition of the survival threshold has been used for evaluating predator-prey system under the effect of polution

(Huaping and Zhien, 1991). Instead of defining the threshold as the lowest probability of a population's ability to survive, their definition was not different from the extinction threshold as shown in Fahrig (2002). Additionally, the use of the survival threshold in their model did not reflect how the model could be used for highly endangered species such as tigers. Thus, a new definition of the survival threshold will be meaningful for the conservation of the Sumatran tiger and other large-bodied predators in general. The practical measure of the $P_S thresh$ is defined by the value of $\mathrm{P}_0 t$ between 95% and 99% as shown in Figure 2.4.

The measurement of the survival threshold ($P_S thresh$) is calculated by a projection of factors being evaluated and the probability of extinction for a certain time horizon ($\mathrm{P}_0(\mathrm{t})$). The $\mathrm{P}_0(\mathrm{t})$ represents the ratio of the numbers of simulations that resulted in extinction and the total number of simulations. The $P_S thresh$ is defined within the interval $0.95 \leq \mathrm{P}_0(\mathrm{t}) \leq 0.99$, and projected into the values of the parameters being tested.

4.3.6 Results

Probability of Extinction

The effect of increased densities of different types of traps on the probability of extinction of the tiger population is shown in Figure 4.15. At the lowest density of traps (0.01 traps/km^2), the probability of tiger extinction varies from 10% for multi-animal traps to 60% for tiger traps. When the trap density was changed to 0.05 traps/km^2, the extinction probability of tigers due to prey trap also increased to 50%, tiger traps to 75%, and multi-animal traps to 37%. A 100% probability of extinction for tigers was reached when tiger traps were dispersed at 0.06 traps/km^2 and multi-animal traps at 0.1 traps/km^2, whereas prey trap scenarios never reached extinction at these values.

The probability of extinction estimated from trap duration showed that only tiger traps were able to reduce the tiger population, with 100% extinction probability. If the tiger trap stayed in the system for 1 month, the tiger trap was able to drive extinction for all simulations. At the highest

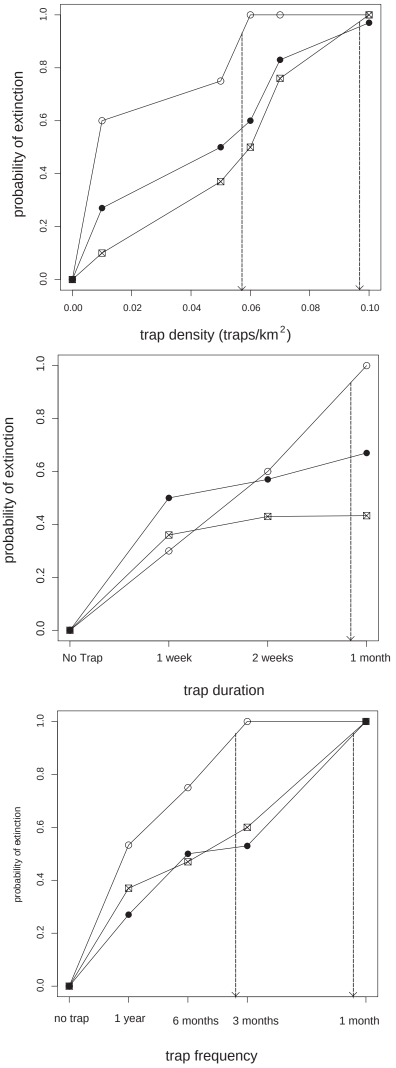


Figure 4.15: Probability of extinction and extinction threshold for each trapping type at different trapping densities, durations and frequencies. The empty circle represents tiger traps, the black circle for prey traps, and the square cross multi-animal traps. The dashed arrow indicates the levels of poaching where the survival threshold occur and corresponds to the parameter values.

trap duration (1 month), the prey traps and the multi-animal traps only produced 57% and 40% tiger extinction probability, respectively. The frequency of traps demonstrated the strongest effect for all trap types. If tiger traps were inserted into the system every 3 months or 1 month(s) during the 20 year simulation, all simulations resulted in 100% tiger extinction. However, prey and multi-animal traps produced 100% tiger extinction if the traps were set in the system monthly.

The three trap types using "extreme scenarios" showed their ability to produce a 100% probability of extinction. All trap types needed a combination of the highest density (0.1 traps/km^2), the highest duration (1 month), and the highest frequency (1 month) to result in a 100% probability of tiger extinction. At medium and low "extreme scenarios", not one trap types reached 100% extinction, illustrated in Figure 4.16.

Survival Threshold

The survival threshold of the tiger population within 20 years of simulations varied with respect to trap parameters. Figure 4.15 shows the region where the survival threshold might occur for each trap types for different trap parameters. Using trap density, all scenarios in the prey trap did not results in a 100% of extinction probability. The highest probability of extinction using this scenario is 97%, where tiger and multi-animal traps placed tigers at the extinction level. The region of survival threshold for the tiger trap occurs between 0.05 to 0.06 traps/km^2, whereas the threshold is located between 0.07 and 0.1 traps/km^2.

Using trap duration scenarios, the only scenario that reached a 100% probability of extinction is the tiger trap at a duration of 1 month in the system. Hence, the region of the survival threshold may occur between a trap duration of 2 weeks and 1 month. Prey and multi-animal traps, at highest trap duration, did not result in 100% probability of extinction. All trap types using the trap frequency parameter resulted in a 100% of probability of extinction. The survival threshold for tiger traps may occur if the tiger traps are only placed in the system ever 3 to 6 months. The survival threshold for prey and multi-animal traps were found at a level where trapping was more frequent than that of tiger traps, as the threshold occurred at 1 to 3 months. The extinction threshold for all three "extreme scenarios" occurred between medium to high values as shown in Figure 4.16. Thus, for further analysis, the highest scenarios were used to test the effectiveness of anti-poaching units to reduce the probability of extinction.

Effect of Anti-poaching Units

Figure 4.16 shows the effect of anti-poaching units (APU) on the probability of extinction for tiger population at different time gaps. The figure clearly shows that tiger traps always results in 100% extinction for all time-gaps of APU. In contrast, to the situation of tiger trap, the APU worked well to reduce the probability of extinction from the prey and the multi-animal traps. The presence of APU less than 1 month after the detection of poaching activities reduced the extinction probability from 100% to nearly 10%, if only prey were poached. The slower the APU to react to poaching the less effect it has on the extinction probability. If the removal of prey poaching was completed within 6 months, the probability of extinction was reduced to nearly 25%. However, if the prey poaching was removed within one year, the probability of extinction was nearly 60%.

The APU for multi-animal poaching clearly showed a similar pattern as that of the prey-trap scenario. The APU reduced the probability of extinction nearly to 20% if the removal of poaching was done within 1 month. Although using a 6 month scenario, the probability of extinction for multi-animal poaching was lower than prey-poaching (17%), and the one-year scenario also lowered the probability of extinction from multi-animal traps to 26%.

4.3.7 Discussion

In ecological systems, the roles of disturbances are important for the dynamic of populations (Hobbs and Huenneke, 1992). The PPP model has successfully demonstrated the effect of disturbance on tiger and prey population through the presence of traps in different level of regimes. The

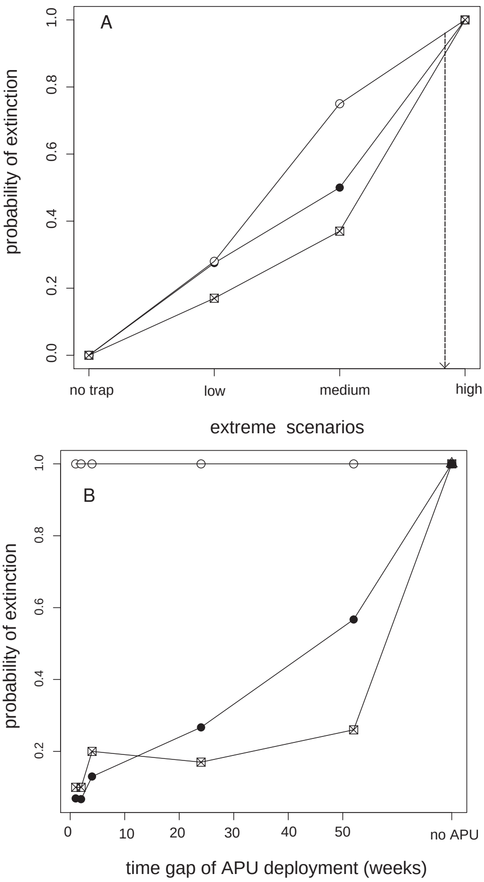


Figure 4.16: Probability of extinction for different trapping types using extreme values (A) and under the effect of different time gaps for the APU (B). The empty circle represents tiger traps, the black circle for prey traps, and the square cross multi-animal traps. The dashed arrow indicates the levels of poaching where the survival threshold occur and corresponds to the parameter values.

introduction of trap parameters in the PPP model provides insight into different behaviour of traps, which was not considered by any previous models. The common approach for testing the effect of poaching and prey depletion were completed by simply reducing a certain number of individual each year from the population modelled Kenney et al. (1995); Karanth and M.Stith (1999); Chapron et al. (2008).

The PPP model introduced three types of traps (tiger, prey, and multi-animal traps) and three trap parameters (density, duration, and frequency), which have important mechanisms that affect the probability of extinction on a tiger population. Three different types of trap which target specific animals have made it possible to test the relative magnitude of the effect of prey depletion, tiger poaching and multi-animal poaching on the survival of tiger populations. This study has showed that tiger poaching has the highest effect on the probability of tiger extinction, in comparison with other trap types. The direct consequence of reduced numbers of tigers due to the presence of tiger traps explains why tiger traps are stronger than prey and multi-animal traps with regards to increasing the probability of tiger extinction. Tiger poaching has been highlighted as the main causal factor for declining tiger populations in the wild. Poaching is mainly driven by the conflict between humans and tigers (Tilson et al., 2010). The conflict between tigers and humans which resulted tiger death, became a common problem in Indonesia and surrounding countries between 1600 to 1950 (Boomgaard, 2001). Nevertheless, the causal factors which determine poaching are various, such as defending humans from tigers, cultural and political purposes, medicinal, and commercial reasons (Boomgaard, 2001; Shepherd and Magnus, 2004; Nyhus and Tilson, 2004b; Tilson et al., 2010).

The results from multi-animal traps was unexpected; previously it appeared to be evident that this type of trap would have a lower effect on extinction than the tiger trap. The initialization of the number of individual of Sambar deer and Red Muntjac were much higher than the tiger population thus making the probability of catching an individual prey also higher than catching an individual tiger. Therefore, the effect of multi-animal trap performed similarly to the prey trap. The random distribution of traps in the system and random prey movement affect the probability of traps to catch tigers. In reality, poachers set traps in a concentrated distribution such as within a certain indidual's home-range (Tilson and Nyhus, 2010; Linkie et al., 2003; Shepherd and Magnus, 2004). Hence, if the distribution of multi-animal trap followed this rule, the probability of catching tiger might be higher. Since both prey species are simulated to move randomly in the system and cannot sense the presence of tigers and traps, they also move into the tiger's home-range, thus distributing the multi-animal traps within a tiger's home-range. This probably still does not increase the probability of tiger poaching, as the potential to trap prey is still higher. Furthermore, the performance of multi-animal traps, which is similar to prey traps, might affect tiger populations on a longer time horizon ($>$ 20 year). Therefore, extending the time horizon of simulation may show a difference between multi-animal and prey traps on tiger population dynamic.

The mechanism of trap densities to affect the probability of extinction was clearly shown for all trap types. A study by Tilson and Nyhus (2010) found that trap densities in the field were set at a rate of 76 steel wires snares for a single female home range, which can be translated into 76 traps/70 km^2 or almost 1 trap per km^2. The results of this study implied that at much lower values of trap density (0.1 trap per km^2) for all trap types can result in a 100% probability of extinction. At the same density and frequency of trap, if traps stayed longer in the system, the probability of catching the targeted animal also increased, thus increasing the probability of tiger extinction. In addition, the more frequent the trap is entered into the system, the shorter the amount of recovery time for tigers overcoming previous trapping disturbances. All trap types resulted a 100% probability of extinction when the trap frequency was monthly. Hence, the trap frequency has a stronger effect on tiger population than trap duration and density.

Most anti-poaching programs assumes that poaching removal will reduce the probability of tiger extinction. This study demonstrated that the anti-poaching program could not reduce the probability of extinction if tiger poaching occurred at a high density, duration and frequency. Although the anti-poaching program was able to reduce probability of extinction caused by the presence of prey and multi-animal traps, precautionary attention should be paid to the fact that the time gap between poaching and program also needs to be relatively short. These findings imply that anti-poaching programs should have a high ability to detect poaching activities and at the same time to remove it in a short time.

The predetermined relationship between breeding tigress and prey density in the prey depletion model of Karanth and M.Stith (1999) implied a strong positive correlation between breeding tigress and prey density. Multiple branching processes with the deterministic model by Chapron et al. (2008) and individual-based model by Kenney et al. (1995) only used one sex class and did not include prey population to predict population extinction. The single-sex approach and exclusion of prey in their model has reduced the complexity of the model, but at the same time it looses the most important environmental factors for tigers and the processes between them. The PPP model improved upon the limitations of these models by the inclusion of all important traits and behaviours for tigers with its relation to prey and poaching. In addition, the trophic interaction between habitat-prey-tiger improved in the existing TIGMOD model by Ahearn et al. (2001). However, since the PPP model requires fine details about individuals and behaviours for population persistence assessment, the computational cost of this model was a tradeoff.

The home range of individual is known to affect the emergence of mammal populations (Wang and Grimm, 2007). The integration of spatial distribution among individuals of tigers is one of the advantages of the use of IBM to test the effect of poaching for the persistence of tiger populations. The PPP model simulated adult individuals with home range as well as adult and sub-adult tigers searching space the establishment of a home range. When an adult individual was poached, its home range is empty and home range seekers might occupy it. In addition, the PPP model includes the emigration processes through the lost of individuals due to failure to establish territory, but excludes immigration processes, which probably affects the results. The absence of immigration affects the dynamics of tiger populations. Hence, incorporating tiger immigration will probably increase the survival levels for tigers, based on the assumption that the simulated population will connect with the immigrating individuals.

Spatial environmental variation, such as elevation, terrain, and access to water explain the mechanistic behavior of home range maintenance for wolves and coyotes (Moorcroft and Lewis, 2006). In addition, landscape structures play an important role in population dynamics (Fahrig, 2007b). The spatial arrangement of individuals might also be affected by variations in habitat conditions such as tropical forests, agroforestry, agricultural land, villages, and other habitat types. Those habitat types have different particular micro conditions which might limit or accelerate the movement of individuals. Therefore, further integration with spatial arrangement of individual as well as habitat or environmental conditions through a geographical information system (GIS) might improve the performance of the PPP model to project the population persistence of the Sumatran tiger.

Tiger-prey relationships are also spatial explicitly simulated, but the PPP model did not yet test the effect of the prey structure on the persistence of tigers. Prey structure is known to affect predator populations in other species (Rudolf, 2008; Abrams and Quince, 2005; Claessen et al., 2000). Moreover, fragility of juvenille ungulate to predation also emphasized the importance of evaluating the effect of prey structure (Barber-Meyer and Mech, 2008) for a predator population. Thus the evaluation of the effect of prey depletion on tiger population will also benefit from testing prey population structures.

A common approach for evaluating the persistence of a population is the use of extinction threshold. Despite the importance of the extinction threshold for predicting population survival, this measure is mainly based on the effort to avoid extinction of a population at the lowest probability of extinction. Human development has affected many large-bodied predators and thus, these animals face a higher risk of extinction than those of a smaller size (Cardillo et al., 2005). The use of extinction threshold might be meaningless due to the higher probability of extinction as a result of intrinsic and extrinsic factors. In addition, the application of an extinction threshold for evaluating the effect of habitat amounts on a certain population (Fahrig, 2002; Lande, 1987; Grimm and Storch, 2000), created the impression that this measure can only be used to evaluate the effect of habitat amounts but not appropiate for others factors, such as human conflict, edge effect, and/or landscape configurations. These factors have been recognized as important factors for large-bodied predators inhabitating a small reserve and surrounded by different land-use types (Woodroffe and Ginsberg, 1998; Parks and Harcourt, 2002; Russell et al., 2003). In the conservation of highly threatened species like tigers, investigating whether the population still has the probability to survive and define suggested conservation action to avoid 100% extinction might provide a realistic solution.

The measure to estimate survival threshold is a reverse measure of the extinction threshold. However, the use of the projection of probability of extinction from factors being assessed is similar to the methods suggested by Fahrig (2002) for the extinction threshold. This method is straightforward only for an unstructured population (Hildebrandt et al., 2006). The PPP model is a structured population consisting of tigers with different ages, age-classes, and sex. Thus, considering a method to detect and visualize survival threshold as suggested by Hildebrandt et al. (2006) and Grimm and Storch (2000) will probably improve the measure of the survival threshold and will be a more useful approach for tiger conservation.

Conservation Implication

The PPP model has displayed the magnitude and the mechanism of the effect of tiger poaching, prey depletion and their combination for Sumatran tiger population's probability of extinction. The model clearly depicted that tiger poaching is the strongest among other types of poachings. The frequency of poaching to perturbate tiger and prey populations is also the strongest factor among poaching parameters to determine the extinction probability of tigers. The PPP model provides a novel approach for evaluating anti-poaching program, which are commonly believed to ensure tiger population persistence. The simulation results suggested that the removal of poaching depends on the type of trap and the time gap between the occurence of poaching and the anti-poaching program's application. Hence, anti-poaching programs should improve the ability to detect the presence of poaching and to disarm poaching in protected areas.

4.4 The Influence of Agroforest and Other Land-use Types on the Persistence of a Sumatran tiger (*Panthera tigris sumatrae*) Population: An Individual-Based Model Approach

Muhammad Ali Imron, Sven Herzog, Uta Berger

Summary: The previous section presented the application of the PPP model for testing the effect of poaching and anti-poaching on the persistence of Sumatran tiger populations. This section demonstrates the use of the PPP model to investigate the effect of landscape composition on the probability of extinction and time to extinction for Sumatran tigers.

An earlier version of this chapter was presented at the World Agroforestry Congress in Nairobi, August 2009. A slight modification of this section was published in the *Journal of Environmental Management*. Published online 22 October 2010, DOI 10.1007/s00267-010-9577-0, http://www.springerlink.com/content/l41444766772924v/

Abstract The importance of preserving both protected areas and their surrounding landscapes as one of the major conservation strategies for tigers has received attention over recent decades. However, the mechanism of how land-use surrounding protected areas affects the dynamics of tiger populations is poorly understood. We developed Panthera Population Persistence (PPP) - an individual-based model - to investigate the potential mechanism of the Sumatran tiger population dynamics in a protected area and under different land-use scenarios surrounding the reserve. We tested three main landscape compositions (single, combined and real land-uses of Tesso-Nilo National Park and its surrounding area) on the probability of and time to extinction of the Sumatran tiger over 20 years in Central Sumatra. The model successfully explains the mechanisms behind the population response of tigers under different habitat landscape compositions. Feeding and mating behaviours of tigers are key factors, which determined population persistence in a heterogeneous landscape. All single land-use scenarios resulted in tiger extinction but had a different probability of extinction within 20 years. If tropical forest was combined with other land-use types, the probability of extinction was smaller. The presence of agroforesty and logging concessions adjacent to protected areas encouraged the survival of tiger populations. However, with the real land-use scenario of Tesso-Nilo National Park, tigers could not survive for more than 10 years. Promoting the practice of agroforestry systems surrounding the park is probably the most reasonable way to steer land-use surrounding the Tesso-Nilo National Park to support tiger conservation.

4.4.1 Introduction

The importance of managing protected areas together with the surrounding landscape is a central issue for the conservation of large endangered mammals such as the Sumatran tiger (Johnson et al., 2006; Nyhus and Tilson, 2004b; Kusters et al., 2008). As a large carnivore, the Sumatran tiger requires large protected areas for habitat, food availability and reproduction. The social, political and economic realities of many landscapes in Asia have turned large suitable habitats into small, fragmented ones (Nyhus and Tilson, 2004b) and the difficulty of halting forest loss has made the situation even worse (Kinnaird et al., 2003). Therefore, the need for integrated and comprehensive management strategies that take into account the complexity of landscapes surrounding protected areas has become more urgent over recent decades.

In order to integrate the surrounding landscape with protected areas, particular attention should be paid to the landscape structure. Landscape structures play an important role in population dynamics (Fahrig, 2007b) with landscape composition providing different risks and benefits to maintain wildlife populations. Sumatran tiger populations have been facing habitat fragmentation and possible population isolation due to forest conversion over the last three decades (Franklin et al., 1999). As a result, the landscape of Sumatra is comprised of many land-use types such as logging concessions, agriculture, settlements, oil-palm plantations as well as mining operations. A challenge for conserving the Sumatran tiger is to understand how tigers respond to those land-uses and which landscape configurations are able to support tiger populations.

The response of tigers to different land-use types should consider their relation to prey species. As a carnivore, tigers depend on prey populations (Miquelle et al., 1999a; Ramakrishnan et al., 1999; Karanth and M.Stith, 1999; Karanth et al., 2004). However, the response of predators to the loss and fragmentation of habitat depends on the complex interaction between predator, prey and their habitat (Ryall and Fahrig, 2006). Therefore, in order to be able to understand the response of the Sumatran tiger to a heterogeneous landscape, we have to understand the mechanism of individual behaviour and the relation with prey distributions and landscape configurations.

To the best of our knowledge, it is hard to find any information on the mechanisms behind the response of the Sumatran tiger to a heterogeneous landscape. Several studies have shown the distribution pattern of the Sumatran tiger and its prey in different habitat types, such as tropical forest within protected areas (Franklin et al., 1999; Kinnaird et al., 2003; Linkie et al., 2003; O'Brien et al., 2003), areas with agroforestry (Nyhus and Tilson, 2004b), palm oil plantations (Maddox et al., 2007) and logging concessions (Linkie et al., 2008). However, those studies did not explain the mechanistic process involved in responding to different habitat types.

In addition, the cryptic characteristics of the tiger and the complexity of the existing landscape configuration have resulted in very few behavioural studies of this species, presenting us with further limitations to understanding their response to habitat change.

Considering the rapid loss of tropical forests on the Island of Sumatra, the emergence of various habitat types surrounding protected areas and the lack of knowledge on the response of tigers and prey to various habitat types, we require an alternative approach to deal with this situation. The approach should be able to be used to understand individual behaviour as influenced by different landscapes. Modelling is one possible approach for predicting population consequences from landscape structure. Individual-based modelling (IBM) has been used to deal with individual behaviour patterns and their emergence at higher levels such as the population or landscape level. IBMs have the ability to simulate the behaviour of individuals and predict interactions depending on complex environmental conditions (Ahearn et al., 2001; Grimm and Railsback, 2005). It is almost impossible to set up experiments with different land-use types surrounding a protected area to monitor the response of tiger populations. The use of IBM would therefore appear to be a promising option that would complement existing monitoring programs. For these reasons, IBM was chosen for this study as a tool for understanding the response of tiger populations to very dynamic changes in land-use.

4.4.2 Methods

Study Area and the development of land-use map

We selected the Tesso-Nilo National Park and its surrounding landscape with a total size of 3,841 km^2. The national park is situated in the lowland area of Riau province in Central Sumatra, Indonesia. The park was established in 2004 and was formerly an area designated for logging concessions. The park is surrounded by different land-use types as shown in Figure 4.17. We developed a land-use map from a satellite image of LANDSAT (Path 126 row 60 date 07 August 2005). To adjust it to the current situation of the study area, we compared it with a land-cover map from WWF-Riau and a ground check was conducted in November and December 2009. We classified the study area into six major land-use types: tropical forest, logging concessions, agroforestry, acacia (*Acacia mangium*) plantations, palm-oil plantations, and settlements.

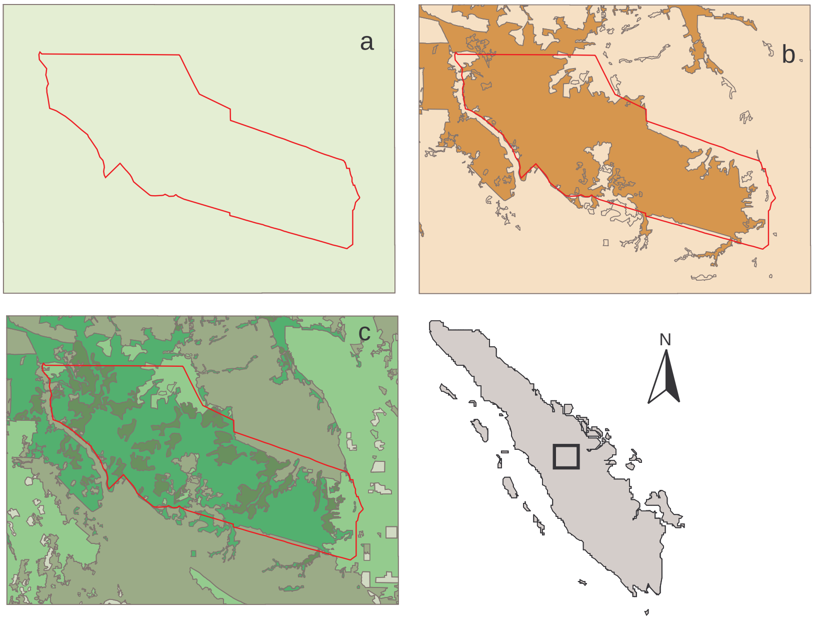


Figure 4.17: Initial conditions of three different landscape compositions: a) single land use b) combined land use c) real land use in Tesso Nilo National Park and the surrounding landscape of Central Sumatra. The red line indicates the border of the park. Different grid cell colors represent different land use types.

Model Description

We developed the Panthera Population Persistence (PPP) model, which was derived from the TIGMOD model (Ahearn et al., 2001). The TIGMOD model was successfully implemented to simulate basic behaviour of the tiger and its potential conflict with humans in Nepal. The model description follows the ODD (overview, design concepts and details) protocol for describing individual- and agent-based models (Grimm and Railsback, 2005; Grimm et al., 2006).

Purpose The purpose of the model is to investigate the potential mechanisms of tiger population dynamics in the reserve under different land-uses.

States variables and scales The PPP model comprises three animal species: the Sumatran tiger (*Panthera tigris sumatrae*) and two of its prey species, the Sambar deer (*Rusa unicolor*) and the Red Muntjac (*Muntiacus muntjac*). The individuals of tigers have different sex and age classes, hunger and starvation levels and reproductive-based state variables. Sambar deer and Red Muntjac have age and hunger levels. Table 4.5 shows the description of state variables for each species in the PPP model. The simulated area is Tesso Nilo National Park and its surrounding landscape (Figure 4.17).

Process overview and scheduling

Ageing As in TIGMOD (Ahearn et al., 2001), tigers and prey increase in age with a time-step of 0.5 days with the age-classes changing accordingly. The age classes and internal state conditions lead to different behaviour patterns such as cubs that only follow the mother or hunger levels which determine whether an individual will hunt or not. Figure 4.18 shows the behaviour of tigers in different age classes within the PPP model.

Movement The PPP simulates two types of movement for tigers; random and directed movement. Random movement is not related to any object. It is part of the behaviour involved in maintaining a home-range, reproduction and parenting. Directed movement includes "following the mother", hunting, mating, and parenting (described below). Appendix C shows further details and parameters. A prey decides to move or to stay based on the habitat quality of the patch.

Table 4.5: Description and units for state variables of individuals in the PPP model

Individuals	State variables	Description	Values and units	Note
Sumatran tiger	age	age of individuals	0-5,400 days	Sunquist et al. (1999); Smith (1993)
	age-classes	classes of age	cubs (0-660 days)	Sunquist et al. (1999)
			sub-adult (660.5-825 days)	Sunquist et al. (1999)
			adult (825.5-5,400 days)	Sunquist et al. (1999)
			old (> 5,400 days)	Sunquist et al. (1999)
	sex	sex classes	male-female	
	hunger level	energy level of an individual	0-100	Ahearn et al. (2001)
	starvation level	starvation level of individual	0-30	Ahearn et al. (2001)
	reproduction-related status	female state variable related to reproduction condition	fertile, infertile, pregnant, parent	Ahearn et al. (2001)
Prey	age	age of individuals	Sambar deer (0-6,120 days)	Nugen et al. (2001)
			Red Muntjac (0 - 3,600 days)	Chapman et al. (2005)
	hunger level	energy level of an individual	0 -200	Adjusted parameter

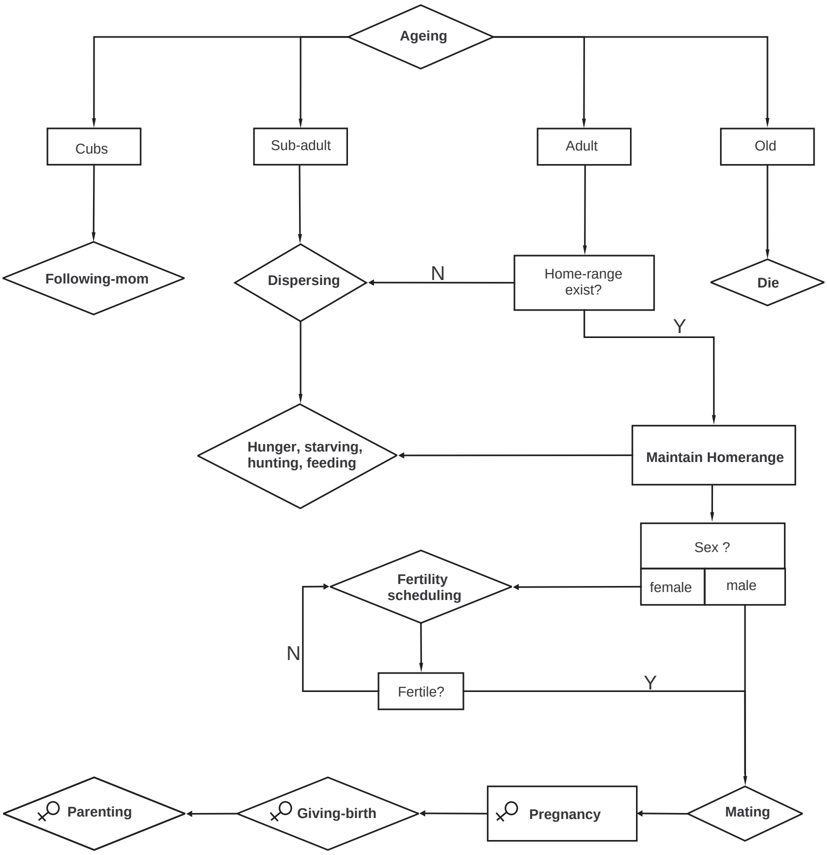


Figure 4.18: Conceptual diagram of main tiger behaviours in different age-classes within the PPP model. The age class determines the behaviour of an individual in relation to its internal states and environmental conditions. The submodel highlighted in bold are explained in detail in the process overview and scheduling.

Hunger and Starvation The hunger level of a tiger starts at 0 and increases by 10 per time-step and by 12.5 for a female with cubs. If an individual has a hunger level above 90, starvation will start. In that case, the hunger level is fixed to 90, and the starvation level increases by 0.5 per time step. If a tiger reaches a starvation level of 30, it will die. When hunger levels are > 60, hunting is stimulated. The hunger levels of a tiger will decrease when it has successfully caught and consumed its prey, the starvation level is then set to zero again and the hunger level is reduced by 12.5 per time-step over the entire feeding period. Foraging behaviour of a prey is controlled by its hunger level.

Hunting A tiger searches for prey within a specific hunting radius. When a tiger has sensed its prey, it will change direction accordingly. The hunting success rate of a tiger varies from 5% to 50% (Sunquist, 2010). Hunting success is assumed to be 50% on any hunting occasion. Tigers prefer Sambar deer (Reddy et al., 2004), and if no Sambar deer is available within their hunting radius they will prey on Red Muntjac.

Feeding Tigers stay close to their hunted prey during the feeding time (Sunquist, 1981). The larger the prey, the longer the tiger will stay to consume it. If a tiger successfully kills its prey in a tropical forest, the model simulates two consecutive days to consume a Red Muntjac and seven days for a Sambar deer without interruption. Tigers spend less time consuming prey when kills are made in human-affected areas while in undisturbed areas tigers are more likely to eat more meat and spend more time doing so (Kerley et al., 2002). To incorporate the effect of human-disturbed areas, we reduce the time of feeding on Red Muntjac to 1.5 days and on Sambar deer to 5 days in these areas.

Reproduction The PPP model simulates the reproduction of tigers through three processes: fertility scheduling, mating, pregnancy and giving birth. A female reaches sexual maturity at the age of 825 days (Sunquist, 1981). In this case fertility scheduling is initiated. The inter-estrous interval of a female tiger is around 25 days during which the female is fertile for about 5 days. A fertile female will call to an adult male for mating. However, mating will only occur when hunger levels of individuals are lower than 60 and there is no starvation. The duration of mating is two days (Sunquist, 1981) and the female will have a 50% chance of becoming pregnant. The gestation period for a female is 102-103 days (Ahearn et al., 2001; Sunquist, 1981; Sunquist et al., 1999). A pregnant female has a random probability of giving birth to 1-3 cubs with a ratio of males to females of 1:3. A new-born tiger will usually adopt all characteristics from its mother except for its sex class, age, its hunger level and starvation level. The age of cubs is 0 at the time step of birth. The hunger and starvation levels are also 0 until the cubs reach sub-adulthood. A female with cubs will not display any mating behaviour until the cubs reach sub-adult classes. We simulated density dependent birth rate for both Red Muntjac and Sambar deer.

Mortality A tiger dies due to starvation. If the starvation level reaches $>$ 30, the tiger will die. If the dead tiger is a female with cubs, the cubs will also die. When an adult male tiger dies, the home-range will be occupied by a sub-adult that is searching for a home-range. Prey mortality is due to tiger killing and starvation. The limit of starvation for prey is defined by hunger level > 200.

Dispersal At the sub-adult level, tigers search for a home range. The home range of a male might overlap with that of one or several females but never with the home range of another male. An adult individual without a home range is removed from the model but is not considered as a dead individual. The PPP model calculates this as a dispersed individual.

Design concept The dynamics of the tiger population emerge from the interaction between tiger individuals, prey and habitat. The PPP model explicitly simulates four types of interaction. The first is a prey-habitat interaction, which shows the movement and the foraging behaviour of prey in different habitat types. The prey decides whether to move to the next patch or to stay depending on certain habitat indices. Such indices also determine the energy gained by the prey while foraging. The second type of interaction is a tiger-prey interaction, which represents the behaviour of a tiger hunting prey. The third type of interaction is tiger-prey-habitat, which represents the time taken to consume prey that has been killed in different land-use types. The fourth type is a tiger-tiger interaction, which simulates the behaviour of mating and parental care (between a mother and cubs).

A tiger prefers to kill large prey. However, when there is no large prey in the hunting radius, the tiger will automatically search for small prey. Newborn tigers inherit this preference for large prey. Adult tigers are known to compete for resources and mating (Sunquist, 1981). When an adult individual cannot establish a home range, the model considers it as transient and takes out from the landscape. Tigers are able to detect prey and mate, and a cub senses the presence of its mother to be followed.

Stochasticity is applied to the probability of a tiger to successfully hunt for prey, the probability of becoming pregnant, the number of new cubs and the proportion of male and female cubs. Collectiveness occurs during mating and parenting behaviour. A male and a female will remain together over the mating period, and a female will stay with its cubs until they reach the sub-adult class.

Initialization

An adult male of the Sumatran tiger requires 116 km^2 to maintain a home-range, and 70 km^2 for an adult female (Franklin et al., 1999). Because no data available for the whole area of the Tesso Nilo National Park, the initial population of tigers was set into 1 individual/100 km^2 (Sunquist et al., 1999) with equal composition between male and female (5 males and 5 females). The total 10 individuals was chosen according to the possible number of tigers occupying the Tesso Nilo National Park with an area of approx. 1,000 km^2. The densities of Red Muntjac and Sambar deer in tropical forest were set according to the findings of O'Brien et al.

Table 4.6: Initiation of Sambar deer and Red Muntjac densities in different land-use scenarios

Land-use types	Densities	(ind/ha)	Habitat quality index $\beta 1$
	Sambar deer	Red Muntjac	
Tropical forest	3.96 [a]	0.88 [a]	5
Logging-concession	2.60[b]	0.65 [b]	4
Agroforest	1.95 [b]	0.52 [b]	4
Acasia plantation	1.30 [b]	0.39 [b]	3
Oil-palm plantation	0.65 [b]	0.26 [b]	2
Acasia Settlement	0.13 [b]	0.13 [b]	1

[a] O'Brien et al. (2003),[b]adjusted parameter

(2003). Sambar deer has a density range of 0.88 - 1.42 individuals /hectare and Red Muntjac has a range of 3.96 - 4.44 individuals/hectare. For this study, we used the lowest value for both Sambar deer and Red Muntjac in tropical forest for a conservative purpose. Due to a lack of data for other land-use types, we proportionately adjusted the density of prey according to the habitat conditions as shown in Table 4.6.

Input 203 x 149 grid cells represent the Tesso Nilo National Park and surrounding land-use. Each grid cell represents 12.7 hectares and is specified by habitat quality, which corresponds to the land-use types. We developed three main scenarios (single, combined and real land-use scenarios) to test the persistence of the Sumatran tiger population under different land-use compositions. Details on the description of each scenario are given in Section 4.4.3. The spatial composition of those main scenarios follows the composition of a land-cover map of our study area and can be seen in Figure 4.17.

Submodels We included four main types of prey behaviour: movement, foraging, reproduction and mortality. Prey movement is defined by two main factors: direction and distance. The distance refers to data obtained for red deer movement (Fryxell et al., 2008) which varies from 0.23 - 7 km/day. This variation covers both the encamped mode (more sedentary behaviour) and exploratory mode (rapid directional movement). The direction of movement is driven by habitat quality indices. The probability of prey movement is calculated as follows:

$\alpha = \beta_1/(\beta_1 + \beta_0)$

with α being the movement probability to the next patch, β_1 being the habitat index of the next path and β_0 being the habitat index of the current patch (Table 4.6). If a $\alpha < 0.5$ then the prey will stay in the current patch, otherwise it will move to the next patch. We did not differentiate between the distance and direction for Sambar deer and Red Muntjac.

Red Muntjac starts to reproduce annually from the age of 2 to 4 years with probability of number of litters consisting of 3 individuals. Sambar deer annually reproduce with 1 litter from the age of 2 years to 6 years. Both prey die when they reach a maximum age (approx. 10 years for Red Muntjac and 17 years for Sambar deer), from acute starving (hunger level is greater than 200), and/or are killed by tigers. Both Sambar and Red Muntjac have density-dependent birth rates. Both will continue to reproduce until the population reaches the carrying capacity.

Implementation The model is implemented in NETLOGO v. 4.1. (Wilensky, 1999). Each simulation was carried out for a simulation time of 20 years or until one of the sex classes of the tiger became extinct. We ran each scenario with 100 repetitions.

4.4.3 Scenarios and analysis

Figure 4.17 shows the landscape composition of single, combined and real land-use scenario. The single land-use scenario consists of either settlements (ST), palm-oil plantations (POP), acacia plantations (ACP), agroforestry (AF), logging concession (LC) or tropical forest (TF). These scenarios represent habitat qualities from low to high, respectively. The landscape composition for these scenarios is a homogenous area. The combined land-use scenarios are a combination of tropical forest with settlements (CST), palm-oil plantations (CPOP), acacia plantations (CACP), agroforestry (CAF) and logging concessions (CLC). The proportion of tropical forest to other land-uses is 2,594 km^2 compared to 1,246 km^2.

These combined land-use scenarios scenarios were mainly tropical forest in combination with either settlements (CST), palm-oil plantations (CPOP), acacia plantations (CACP), agroforestry (CAF) or logging concessions (CLC). The proportion of tropical forest in the combined land-use is 2,594 km^2 compared to 1,246 km^2 of other land-use. The forest area follows the distribution of pristine forest and secondary forest in the Tesso Nilo National Park and its surrounding landscape (Figure 4.17). In addition, a real land-use scenario also is used to evaluate the current land-use compositions in the study area. The proportion of the size of each land-use type in the real land-use scenario is given in Table 4.7.

The observation was done by recording the time-step when absolute extinction or quasi-extinction occurs. Three extinction measures : the probability of extinction $P_o(t20)$, the arithmetic mean time to extinction (*Tavg*), and the intrinsic mean time to extinction *Tm*, were calculated. The probability of extinction $P_o(t20)$ represents a ratio between the numbers of simulations resulting in extinction and the total number of simulations in each scenario during 20 years of simulation. The arithmetic mean time to extinction (*Tavg*), the *Tm*, and *Trel* are explained in the chapter 3. For conservation purposes, the intrinsic mean time to extinction is very important to provide a careful prediction. Unlike the arithmetic time to extinction where the initial conditions have an effect on the established phase, the initial conditions of the model do not have any consequences for the relaxation time (Grimm and Wissel, 2004). In addition, to understand how landscape structures affect the tiger population, we also recorded the number of dispersed tigers. This value corresponds to the number of tiger individuals leaving the study area because they are unable to establish a home-range.

4.4.4 Results

Tiger and prey densities at different land use scenarios

Figure 4.19 compares densities of tigers, dispersed tigers and prey population at the end of the simulation in each scenario. In general, the densities of tigers at the end of simulations showed a significant difference for all land-use scenarios (Kruskal Wallis test, H = 772.18, df = 11, $p < 0.01$). Similar patterns could also be seen for the density of dispersed tigers (Kruskal Wallis test, H = 1052.32, df = 11, $p < 0.01$), and for the remaining prey population (Kruskal Wallis test, H = 969.03, df = 11, $p < 0.01$).

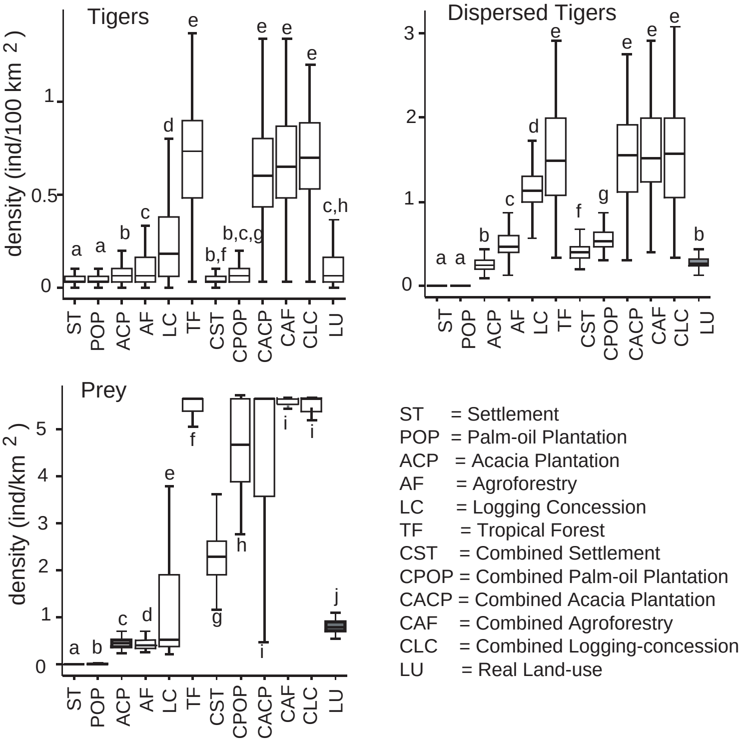


Figure 4.19: Box plot comparison on remained tiger, Sambar deer and Red Muntjac populations when simulation ended and number of tigers lost due to dispersal at different land-use scenarios

We separated the analysis for single and combined scenarios. Under single scenario, a strong significant difference among scenarios was also found for remaining tiger densities (Kruskal Wallis test, H = 318.05, df = 5, $p < 0.01$), dispersed tigers densities (Kruskal Wallis test, H = 556.21, df = 5, $p < 0.01$) and remaining prey densities (Kruskal Wallis test, H = 505.31, df = 5, $p < 0.01$). Among all scenarios, the tropical forest scenario showed the highest values for tiger, dispersed tigers as well as prey densities. The combined land-use scenarios showed that the tiger density differed among scenarios (Kruskal Wallis test, H = 397.50, df = 5, $p < 0.01$), as did the density of dispersed tigers (Kruskal Wallis test, H = 474.53, df = 5, $p < 0.01$) and the remaining prey density (Kruskal Wallis test, H = 322.89, df = 5, $p < 0.01$). No significant different on the densities of tigers, dispersed tigers and prey for combination of tropical forest with acacia plantation, agroforestry and logging-concession.

With the real land-use scenario, the density of tiger was different from all other scenarios except for agroforestry. The remained dispersed tiger densities also showed a significant difference with other scenarios except for acacia plantation. The remaining prey densities showed a significant difference to all other scenarios.

Extinction Probability

The probability of extinction -within 20 years of time simulation $P_o(t<20)$ under a single land-use scenario indicated that the increment of habitat quality reduces the probability of extinction (Table 4.7). Tropical forest was the best scenario with the lowest probability of extinction $P_o(t<20) = 4\ \%$ followed by logging concessions $P_o(t<20) = 66\ \%$, agroforestry $P_o(t<20) = 99\ \%$. Acacia plantation, settlements and palm oil plantations resulted in $P_o(t<20) = 100\%$ extinction over the simulation period.

All scenarios with combined land-use showed a lower probability of extinction than a single land-use. However, combined palm oil plantations and settlement only showed a slight difference from a single scenario. The combined scenario of tropical forest with acacia plantations and agroforestry showed a remarkable improvement in the probability of extinction from

Table 4.7: Number of simulations resulting extinction and arithmetic time to extinction(Tavg) at different scenarios

Scenarios	N	Tavg (years)
Settlement (ST)	100	0.13
Palm-oil Plantation (POP)	100	0.22
Acasia Plantation (ACP)	96	10.83
Agroforestry (AF)	72	14.79
Logging concession(LC)	37	16.31
Tropical Forest (TF)	10	18.97
Tropical forest + settlement (CST)	100	8.90
Tropical forest + Palm oil Plantation (CPOP)	99	10.51
Tropical forest + Acasia plantation (CACP)	19	16.55
Tropical forest + Agroforestry (CAF)	19	17.22
Tropical forest + logging concession(CLC)	8	19.74
Real landuse (LU)	99	7.79

that of the single acacia plantation and single agroforestry scenarios. In addition, combined logging concession and combined agroforestry was similar as single tropical forest $P_o(t<20) = 4\%$, while the real land-use scenario showed $P_o(t<20) = 100\%$ of all simulations resulting in an extinction within 20 years of the simulation.

Time to Extinction

Arithmatic time to extinction Among all single land-use scenarios, tropical forest displayed the highest *Tavg* values whereas settlements showed the lowest. From the combined scenarios, the combination of tropical forest with acacia plantation, agroforestry and logging concessions improved the time to extinction from their single scenarios. The real land-use scenarios were able to support a tiger population with a *Tavg* of 7.31 years (Table 4.7).

Relaxation time The relaxation time was measured only on the scenarios with > 30 simulations which resulted tiger extinction/quasi extinction.

The relaxation time for single settlements required more than one year to relieve from the effect of initial conditions during simulation. The logging concessions scenarios achieved the longest relaxation compared to the other scenarios, followed by agroforestry and acacia plantations respectively (Figure 4.20). The calculation of *Trel* were not applicable due to very low extinction probability of tropical forest within 20 years and very clumped data on palm-oil plantation. The relaxation times for combined scenarios were only calculated for palm-oil plantation (CPOP) and settlement (CST). The relaxation time for the real land-use scenarios was the lowest among all other scenarios (Figure 4.20).

Intrinsic time to extinction In single land-use scenarios, the settlement displayed the shortest *Tm*, whereas the logging-concession showed the longest. Agroforestry and acacia plantation delayed the extinction of tiger populations for more than 5 years. In settlements tigers could only survive for less than 2 years (Figure 4.20). The combination of tropical forest with acacia plantation, agroforestry and logging concessions were not calculated due to low probability of extinction (Table 4.7). Settlements and palm-oil plantation could support tiger populations for more than 5 years when combined with tropical forest. The real land-use scenario could maintain tiger population for not more than 10 years (Figure 4.20).

4.4.5 Discussion

The PPP model is the first spatially-explicit individual-based model that has been developed for understanding the consequence of different land-use configurations on the persistence of the Sumatran tiger population. The model has plausibly simulated important key behaviours of tigers to respond to different land-use types in Central Sumatra. The landscape compositions affected the persistence of Sumatran tiger populations due to three types of mechanisms. The first of these mechanisms are habitat conditions, which affect the numbers of prey available for tigers. The second - prey mortality - is affected by a variation in the food consumption of prey under different land-use types. The third mechanism of human-affected areas reduces the time to consume prey that has been killed by

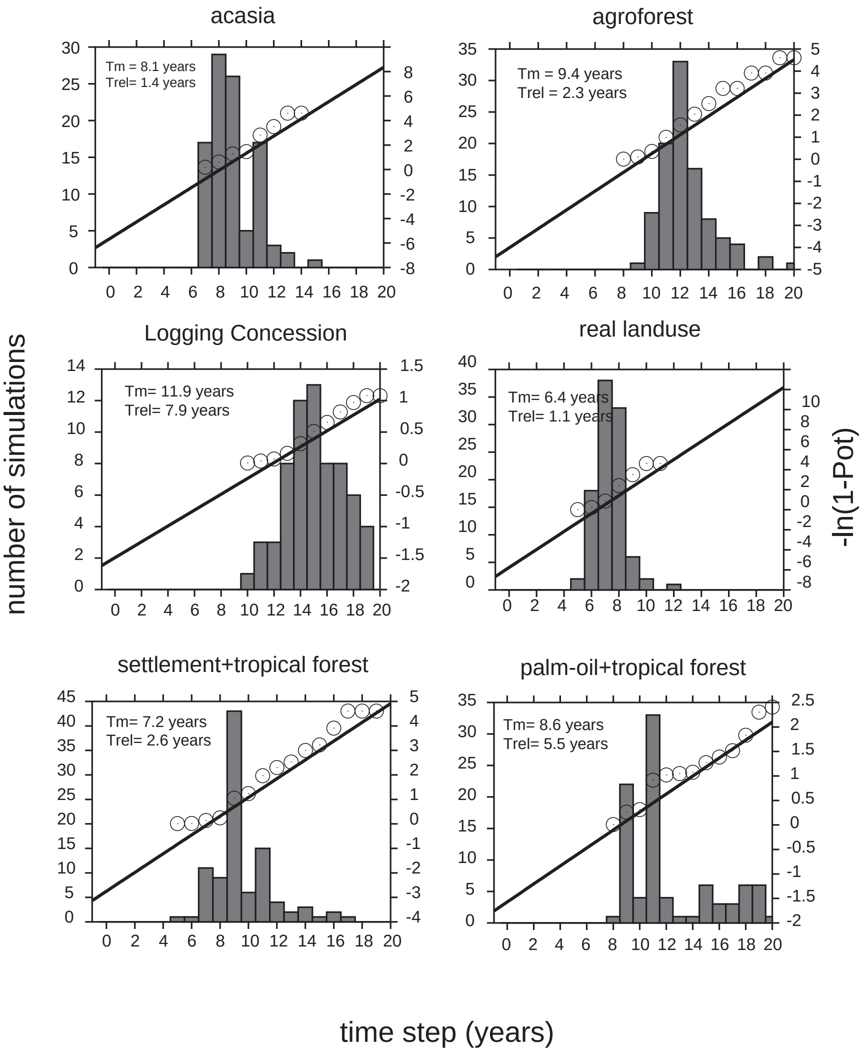


Figure 4.20: Relaxation time and intrinsic time to extinction of single and combined scenarios. Other scenarios are not shown here due to not applicable to calculate both of these measures

the tiger.

Tigers respond to the presence of humans by reducing the time they have to consume prey and by exhibiting a less efficient consumption than in undisturbed areas (Kenney et al., 1995). The PPP model simulated different times for feeding (t-feeding) for tigers in various land-use types. In their natural habitat, tigers use a maximum time for feeding, but in human-affected land-use areas, tigers consume prey with less time for feeding. Consequently, tigers gain less energy in habitats with anthropogenic land-use than in habitats with tropical forest land-use. The direct consequences of an individual gaining less energy results in a higher probability of starvation, eventually leading to mortality. Since the PPP model only simulates mating behaviour when individuals are not hungry and starving, the probability of mating is reduced when less energy is gained by an individual. In turn, this will reduce the probability of reproduction. These two factors determined the probability of extinction as well as the time to extinction in each scenario.

The results from the single scenarios clearly indicate that different habitat qualities are important for population persistence analysis. The PPP model plausibly showed the effect of habitat conditions on the foraging and movement behaviour of prey and the movement and feeding behaviour of tigers. Even though we used an optimistic value for the hunting radius, the results of our simulation still showed that the survival chance was relatively low except under the tropical forest scenario. The tropical forest scenario is the best scenario among all of the scenarios. The model showed that large protected natural landscapes are preferable for tigers to survive and reproduce, in line with the empirical study by Linkie et al. (2003) that tigers are best conserved in large protected areas.

The combined scenarios highlighted the importance of the land-uses surrounding protected areas for tiger conservation (Baeza and Estades, 2010). Although logging-concessions, agroforestry and acacia plantation as single land-use scenarios were not the best habitat for Sumatran tigers, the combination of tropical forest with them resulted in an improved situation. However, since we did not test the simulation for more than 20 years, further analysis beyond this time horizon will be more meaningful.

Among all anthropogenic land-use types, selective logging concessions provided the best alternative to maintain forest cover and ensure the availability of alternative food for prey (Meijaard and Sheil, 2008). In addition, the gaps created from logging provide tigers with the opportunity to have a better access for dispersal and hunting (Linkie et al., 2008). Selective logging concessions close to a protected area provide a good habitat for tigers (Linkie et al., 2008). The fact that Tesso-Nilo National Park used to be logging concessions but is still able to support a tiger population suggests that it is reasonable to combine this type of land-use when it is close to a protected area as part of an overall tiger conservation strategy.

Agroforestry and forest plantations have become increasingly more apparent in the Sumatran landscape. The probability of these two scenarios for the persistence of tiger populations was more than 90% over 20 years if combined with tropical forest. Our findings can be used to explain why agroforestry has the potential to conserve tiger populations in Nepal (Gurung et al., 2008; Dinerstein et al., 1999) and Sumatra (Nyhus and Tilson, 2004b). Agroforestry surrounding strict protected areas can support the conservation of the Sumatran tiger through a greater availability of prey (Nyhus and Tilson, 2004b). The Agroforestry system on the island of Sumatra varies in its vegetation compositions such as rubber (Beukema et al., 2007), multi-storied tree gardens (Michon et al., 1986), Damar /resin production agroforestry (Kusters et al., 2008)as well as coffee agroecosystems (Philpott et al., 2008). These different vegetation compositions might bring about different consequences for both the Sumatran tiger and its prey. A large-scale forest plantation might provide protection from human pressure. However, most forest plantations are managed in a monoculture system, which might not support many species of prey, but could lead to a population explosion for some species, such as wild boar.

The settlement and oil-palm plantation scenarios clearly showed the detrimental effect of these land-use types on tiger persistence. Both single and combined scenarios resulted in extinction within a relatively short period of time. This finding is consistent with the absence or non-detection of tigers in settlements and palm-oil plantations (Maddox et al., 2007). Settlements and oil-palm plantations do not provide good habitat for prey, provide poor habitat and experience high human pressure, leading to the absence of tigers.

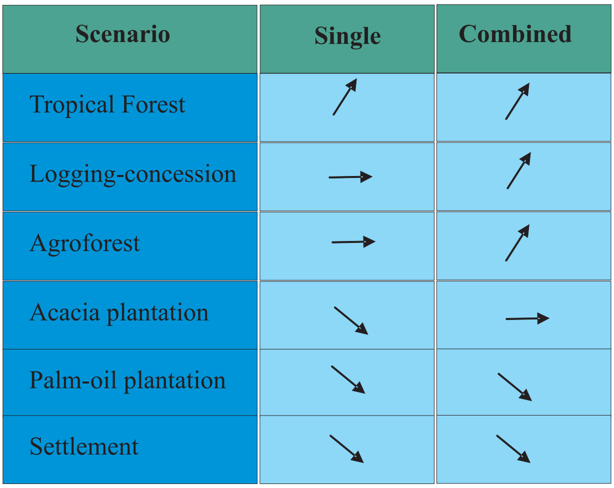
The real land-use scenario resulted in a relatively short time to tiger extinction. A small proportion of tropical forest (6.75%) and a large proportion of settlements and palm-oil plantations (32.2%) might explain the disappearance of tigers due to a low density of prey (see Table 4.6). However, since the PPP model integrated a land-cover map which is not directly represented by a habitat-matrix map for prey species, the incorporation of a habitat suitability index map might improve the prediction. In addition, the pressure from poaching under anthropogenic land-use scenarios is crucial for the persistence of both tiger and prey (Nyhus and Tilson, 2004b). Therefore, to improve our understanding of the effect of these land-uses, poaching should also be included.

The PPP model simulated the response of both tiger and prey on the presence of anthropogenic land-use. However, we assume that the movement decision of both Sambar deer and Red Muntjac are the same. However, different body size and ability to adapt to the presence of human probably affect the movement behaviour. Studies have shown that the movement decisions of individuals are important factors for populations of the lynx (Kramer-Schadt et al., 2004) and the Florida panther (Cramer and Portier, 2001). Therefore considering species-dependent movement decision of prey would be worth in the next model development.

4.4.6 Conservation implications

The PPP model successfully simulated the response of tigers and their prey to various land-use types. The model demonstrates the mechanisms of how tigers and their prey are affected by different land-use scenarios. The PPP model proves that tropical forest is the best scenario. However, with the current rates of tropical deforestation on the island of Sumatra, a large tropical forest area is rarely found in a real situation. The PPP model also showed the importance of including logging concessions and agroforestry in the overall conservation strategy for the tiger. However, the potential detrimental effect such as that from poaching should be considered.

Table 4.7 The effect of all land-use scenarios on population persistence are symbolized by the arrow direction. The arrows pointing upwards represent good scenarios for the Sumatran tiger, horizontal arrows are relatively neutral and arrows pointing downwards are bad scenarios for the tigers.



Scenario	Single	Combined
Tropical Forest	↗	↗
Logging-concession	→	↗
Agroforest	→	↗
Acacia plantation	↘	→
Palm-oil plantation	↘	↘
Settlement	↘	↘

Despite the ability of acacia plantations surrounding a protected area to extend the time to extinction, due to its potential bad effect from monoculture practices, this land-use type is not recommended to be established surrounding a reserve. Both palm-oil and settlement scenarios, either on their own or combined with tropical forest do not support tiger conservation. Therefore, avoiding these land-use types from surrounding a protected area can help to reduce the probability of local extinction (Table 4.7).

Our findings highlight the importance of logging concessions and agroforestry surrounding a protected area for the conservation of the Sumatran tiger. Agroforestry provides ecological services through corridors and food sources for the tiger and its prey. This study shows the critical condition of the land-use composition surrounding the Tesso-Nilo National Park. A low proportion of natural areas together with a large proportion of human-affected areas are critical factors affecting the tiger in the Central

Sumatran landscape. Under the assumption that the re-establishment of natural, undisturbed forests in the region is unrealistic, the most feasible way to improve this condition is to promote the practise of agroforestry systems surrounding the park, while at the same time reducing poaching.

Chapter 5

General Discussion

Summary: The previous chapter presented the results this study which have been published or prepared for publication. This chapter starts with a small review of the main findings which are presented in the Section 5.1. The strengths and limitations of the construction and use of the PPP model to address research questions and challanges in the science of tiger conservation are discussed in the Section 5.2.

5.1 Main results

The main results of this study are as follows:

1. The sensitivity of the outputs of the PPP model varies depending on particular parameters. For instance, the number of tigers and prey killed were sensitive to the time required by tigresses to care for their cubs (T_{fol}); the number of dispersed tigers was highly influenced by a change in the hunting radius (Ht_{rad}) values, while the number of prey was sensitive to the Red Muntjac growth rate (G_m).
2. The relationship between prey and tiger in the PPP model is confirmed by a range of empirical studies on the average number of prey killed by tiger per year. Thus, the construction of the PPP model provides a proper theoretical and operational framework to be used for both hyphothesis testing and the application of conservation programs.
3. Habitat quality plays an important roles in prey mortality and migration. The better the quality of habitat, the more prey survive, the lower the level of emigration, and thus, more prey is available for tigers.
4. The effect of landscape configuration on prey mortality and migration depends on the habitat quality of the landscape. The lower the quality of the habitat surrounding the best habitat patches, the greater the rate of prey emigration, and therefore, the lower the number of surviving prey, and finally, a reduction in the number of prey available for tiger predation.
5. Optimum movement behaviour of prey allows for a low number of migrating prey and a high-level of prey survival which is available for tigers.
6. The magnitude of tiger poaching was the strongest in comparison with other poaching types. The poaching frequency was the most forceful parameter affecting the probability of tiger extinction in comparison with other poaching parameters.

7. The ability of anti-poaching programs to detect and disarm poaching are key factors for ensuring the persistence of the Sumatran tiger experiencing poaching effects.

8. Land use surrounding a protected area plays an important role in determining the persistence of the Sumatran tiger through mechanisms based on the response of tigers and prey to different land-use types.

9. Existing landscape configurations could not support Sumatran tiger long-term population persistence in the Tesso-Nilo National Park and surrounding landscape. The incorporation of agroforestry near the park is the best reasonable and suitable landscape configuration for the survival of the tiger population.

5.2 Discussion of the results

The PPP model is a novel approach for the conservation of the Sumatran tiger. The individual-based model, as described in the PPP had not been previously considered as a tool for Sumatran tiger conservation. Thus, the construction of the PPP model is still in its early stages of development. The strengths and weaknesses of the PPP model to answer the urgent questions, to support management decisions, and to address the research questions in this dissertation are discussed in following sub-sections.

5.2.1 What is new in the PPP model ?

The PPP model is the first application of the individual-based modelling approach for the conservation of the Sumatran tiger. The existing PVA models did not consider individual variation and response to the factors (habitat loss and destruction, tiger poaching and prey depletion) contributing to the persistence of the Sumatran tiger. In contrast, the structure of the PPP model allows for explicit consideration of individual behaviours and demographic stochasticity (DeAngelis and Mooij, 2005; Grimm, 1999). The inclusion of important traits and behaviour of tiger and prey at fine temporal and spatial scales force the mechanism in the population dynamics of tigers and their prey.

In comparison with other models for Sumatran tigers, the complexity of the PPP model is relatively high. The PPP model includes 29 parameters, whereas other models, such as the GIS model for predicting the presence of tigers, only involved less than ten parameters (Linkie et al., 2006; O'Brien et al., 2003; Kinnaird et al., 2003). The inclusion of all tiger age classes and their specific behaviours successfully identified essential processes which determine Sumatran tiger population persistence. This approach allows testing of alternative hypotheses on the mechanism of particular behaviour to the population dynamics as demonstrated in Section 4.2, as well as testing the effectiveness of management options such as in Section 4.4 and 4.3. However, these fine scale of traits and behaviours of tiger and prey have drawbacks due to expensive computational cost during simulation.

Predetermined relationship between factors, such as a strong relationships between tigress and prey populations (Karanth and M.Stith, 1999; Chapron et al., 2008) have limited the conventional PVA models to be used to understand or test ecological hyphoteses (Lindenmayer et al., 1995). Indeed, the PPP model also included explicit relationships between individuals and their environment. However, the population dynamics of the PPP model were not mainly a source of the predetermined relationships in the model. The use of the sensitivity analysis to evaluate the performance of the PPP's output depended on random changes in values for all input parameters. Section 4.1 illustrated that the population dynamics of the Sumatran tigers in the model are a results of bottom up mechanisms of individual behaviours.

The lack of ability of traditional PVA models to include environmental variation, such as habitat change (Boyce, 1992; Lindenmayer et al., 1995) have limited their use for management practices for instance evaluating landscape planning. Current models for Sumatran tigers have linked geographic information systems (GIS) and the population viability analysis of tigers (Linkie et al., 2003; O'Brien et al., 2003; Uryu et al., 2007). However, their approaches were less suitable for tiger management due to a lack of explicit mechanisms between landscape configuration and the persistence of tigers (Kareiva and Wennergren, 1995). The PPP model was spatially explicit constructed, allowing for the integration of maps into the model, and interactions between individuals and their abiotic factors, represented by habitat quality in each grid cell. The model can also be used to understand mechanisms between landscape configuration and tiger populations. The simulation of both movement decisions and feeding behaviours at a temporal resolution of 0.5 days per time step, can provide the best explanation of the mechanism of tiger response to different land-use qualities and configurations as can be seen in Section 4.4.

This study introduce survival threshold as a new measure for the conservation of large-bodied predators that are under high-level pressure from human developments such as the Sumatran tiger. The survival threshold is a reverse value, derived from the extinction threshold under the effect of different factors. The survival threshold value provides a quantitative measure for predicting the effect of different factors such as poaching, the level of human-tiger conflicts, and habitat amounts, for the probability of tiger extinction. However, the use of the projection of probability of extinction from factors being assessed is similar to methods suggested by Fahrig (2002) for the extinction threshold. This method is straightforward but only for an unstructured population (Hildebrandt et al., 2006). Since the PPP model consist of structured tiger population consisting tigers with different ages, age-classes, and sex, considering a method to detect and visualize survival thresholds, as suggested by Hildebrandt et al. (2006) or Grimm and Storch (2000) will probably improve the measure of the survival threshold and will be a more useful approach for tiger conservation.

5.2.2 Insight into Predator-Prey Models

The predation pattern produced by the PPP model confirmed previous studies on prey consumption rate of tigers as demonstrated in Section 4.2. This finding confirms the suitability of individual-based model approaches for simulating the predator-prey relationship. Thus, further applications for practical conservation, such as for testing different tiger conservation paradigms (Section 4.3) and landscape configurations (Section 4.4) were built on a strong foundation.

The use of the PPP model to test two mainstream tiger conservation paradigms is one of the advantages of this study. However, the PPP model may underestimate the effect of tiger poaching on total number of tigers, as it did not include the effect of tiger poaching on *infanticide* especially with regards to reductions in the number of male cub. Infanticide has been discovered for lions, it is currently unknown if tigers also exhibit this behaviour. Thus, any study providing clues about the rate of *infanticide* in tigers, which could then be considered in the model, will enhance the performance of the PPP model and the study of tiger ecology and behaviour in general.

The sensitivity analysis of the PPP model is an important achievement to gain insight into predator-prey relationship through modelling. Section 4.1 showed that the number of dispersed tigers was highly influenced by the ability of individual tigers to detect the presence of prey directly related to the hunting radius (Ht_{rad}). Similar findings have also been reported for the lynx (Kramer-Schadt et al., 2004) and the Florida panther (Cramer and Portier, 2001). These studies showed that the individual ability to perceieve landscape were influential factor for the number of dispersed individuals. However, the expression of perceptual distance in these three models are different. Both the lynx and the Florida panther models define perceptual distance as the ability of individual to percieve landscape for dispersal, whereas the PPP model determines the perceptual distance as the distance from tiger to prey. The difference in the definition of perceptual distance of predators becomes more complicated if different predator-prey systems are compared, for example the backswimmer model of NFM (Gergs and Ratte, 2009; Gergs et al., 2010). Although using a similar model structure to that of the PPP model which included predation behaviour, the NFM defined perceptual distance as the three dimensional distance from backswimmers to the prey, where the nature of water system is expressed as a water colum in three dimensional space. Different concepts about the expression of indidual perceptual distance create an opportunity for further study that focuses on this concept in different predator-prey systems and models.

The perceptual distance of predators is not only hampered by different definition among systems and models, but also a lack of empirical data to support the theory, particularly for cryptic species such as the tiger, lynx, and Florida panther. Studies on the perceptual distance for these three species were hard to find. However, for smaller and simpler predator-prey systems such as backswimmers (Gergs and Ratte, 2009; Gergs et al., 2010) and raptors (Andersson et al., 2009), empirical data from laboratory and field experiments are available. Recent studies showed that animal body masses might play a role in the utilisation of space (Jetz et al., 2004) and that encounter distances can be expressed as a function of insect larval stage (Gergs and Ratte, 2009). Furthermore, Kooijman (2000) suggested that life history traits, such as the ingestion rates, are generally proportional to the body size of an animal. Such studies might indicate possible relationships of scale between hunting distances and the body sizes of predators. For the parameterisation of individual-based predator-prey models, further studies involving different taxonomic groups and predator-prey systems are urgently needed to test this rule and to deduce general rules for extrapolation between species.

5.2.3 Contributions to Model Analysis of Individual-Based Models

Model analysis in individual-based models consists of different techniques, such as the robustness test and sensitivity analysis. The later is less recognized for the individual-based modelling for ecology due to its expensive computational cost, missing links between the purpose of IBMs and the inferences taken from the results of sensitivity analysis, as well as the usefulness of robustness tests for IBMs (Grimm et al., 2006). The application of the Morris Method (Morris, 1991) has opened opportunities to perform sensitivity analysis for a relatively highly complex PPP model, while incurring a relatively low computational cost. The use of the screening design in the Morris Method provided an alternative to other approaches, such as quantitative and expensive computational approaches for evaluating the sensitivity analysis of model output at the early development of any IBMs. The sensitivity analysis, using the Morris Method's screening design revealed the relative importance of model parameter for specific model outputs in the PPP model. This is an important achievement in the analysis of IBM, as other models were only able to perform sensitivity analysis using traditional one-factor-at-time for specific parameters such as poaching in the tiger poaching model (Kenney et al., 1995) and the human conflict parameter in the TIGMOD model (Ahearn et al., 2001).

5.2.4 Understanding the Individual Response Mechanism on the Heterogenous Landscape

The construction of the PPP model has gained two main achievements with regards to understanding tiger response mechanisms on a heterogenous landscape. The first relates to the representation of the landscape. The landscape in the PPP model is not only represented by a habitat-matrix but also by habitat-matrix-semi habitat. The use of habitat-matrix-semi habitat, which represents different habitat qualities and landscape configurations play an important roles in the dynamics of metapopulation (Moilanen and Hanski, 1998). The representation of habitat in most generic PVA models such as ALEX, RAMAS, GAPPS and VORTEX rely on the classical metapopulation theory which assume that a population occupies different habitat patches and are surrounded by a landscape matrix (Fahrig, 2007a). This approach neglects landscape configuration, which might not only consist of a habitat and matrix, but also of different qualities of habitats. In addition, the survival of a population is determined by the distance between habitat-patches in the classical metapopulation theory. Different habitat qualities can affect a species due to risks and benefit which are percieved by the animal (Fahrig, 2007b; Russell et al., 2003; Nathan, 2008; Wiegand et al., 1999; Umetsu et al., 2008). Moreover, if a habitat quality is decreasing and later improved through habitat restoration, the population often cannot quickly recover and results in a time delay (Schrott et al., 2005). This time delay in population recovery in relation to habitat quality and landscape configuration are seldom considered. Hence, the representation of different habitat qualities in the landscape (Section 4.2 and Section 4.4) demonstrated that the PPP model considered important factors in population dynamics, with regards to habitat quality and landscape configuration.

Second, the PPP model simulates individual behavioural response to different habitat qualities in the landscape. Section 4.2 confirms that a small difference in movement behaviour can affect the dynamics of a prey population (Hawkes, 2009). The movement behaviour of tigers and prey in the PPP model included four main aspects in the ecology of movement(Nathan, 2008), including movement motivation, navigation capability, motion capacity and external environmental conditions. Additionally, feeding behaviour of tigers in different land-use types have emerged in the population dynamics of tigers within landscape configuration as demonstrated in Section 4.4. The use of the IBM approach within the PPP framework and the inclusion a high-level of details about individual traits and behaviour has covered almost all important process in population dynamics, except immigration as presented in Sections 4.2 and 4.4. Therefore, the immigration process should be incorporated into the PPP model in the future.

One important effect of landscape fragmentation relates to genetics variations of a given species that reflects long-term consequences of the habitat's configuration. Studies showed that habitat fragmentation has a pronounce effect on the genetic variation within a sub-population and among sub-populations of large mammals. Studies on how the effect of the development of highways and road affected genetics flow between sub-population of Red Deer in Germany (Herzog and Gehle, 2001; Gehle and Herzog, 2003; Imron and Herzog, 2009). Furthermore, the effect of fragmentation also lowered genetic variations of a smaller population of the Florida Black Bear and the genetic difference is strongly exhibited between sub-populations (Dixon et al., 2007). Therefore, the PPP model should incorporate a larger geographical range to allow for simulation of genetics flow between sub-populations and to measure the potential effect of habitat fragementation on the Sumatran tiger population.

5.2.5 Contributions to Conservation

The PPP model is not a generic PVA model like the VORTEX, RAMAS, GAPPS, INMAT and ALEX which can be used to assess population viability across different taxa and geographical ranges (Lindenmayer et al., 1995; Brook et al., 1999). The PPP model was constructed with the aim to understand the bottom-up mechanisms of interactions between individuals and their environments on the population dynamics of the Sumatran tiger in central Sumatra. Dense information about individual traits and complex processes for individual Sumatran tigers and prey has the consequence that the use of the PPP model for other species should adjust multiple parameters and processes. Thus, the PPP model is specific for assesing the consequences the population level of individual tiger behaviours. In addition, the parameterization of the landscape using Tesso-Nilo National Park in the PPP model also implied that additional effort should be invested to prepare appropriate maps using GIS if the PPP model is to be used for other geographical areas.

Despite the limitations described above, the PPP model contributed significantly to fill gaps in the science of Sumatran tiger conservation. The three most important factors for tiger conservation (prey depletion, tiger poaching, and habitat destruction) have been assessed through the use of IBM. The PPP model demonstrated the evaluation of two existing polar paradigms of tiger poaching and prey depletion in Section 4.3. This section also raised our awareness about the possible consequence of the presence of a combination of these two paradigms for tiger conservation practices in Sumatra island. In addition, this study also provides insight into the consequences of extinction probability after anti-poaching programs have been carried out. Findings from Section 4.3 highlight the important effect of tiger poaching in comparison to prey depletion. Also, poaching characteristics determined the probability of tiger extinction. The evaluation of the effectiveness of anti-poaching programs to reduce the probability of extinction revealed that the ability of anti-poaching units to detect possible poaching and disarm poaching are key points for a successfull conservation program.

Despite the limitations for wider geographical applications, the integration of the PPP model with land-use realities map in central Sumatra makes this approach is useful for local Sumatran tiger conservation practices. The conservation of endangered species, such as the Sumatran tiger, requires application at the local level which also involves local stakeholders. The use of local specific details such as land-use types surrounding a protected area in central Sumatra provide a very useful approach for building local support for tiger conservation. Hence, the PPP model is not only addressing scientific questions but is also useful for practical conservation on a local scale.

The representation of the landscape using a habitat-matrix-semi habitat have addressed the limitations of conventional PVA models (Fahrig, 2007a). Sections 4.2 and 4.4 presented the results of the effect of different habitat qualities which is also represented by land-use types as well as landscape configuration on prey and tiger populations. Using static landscape configuration, the PPP model successfully evaluated the response of individual mechanism in a heterogenous landscape. However, landscape in Sumatra has become highly dynamics within the last 30 years (Dinerstein et al., 2006; Uryu et al., 2007; Gaveau et al., 2009). The success of the implementation in the static landscape has provided a strong foundation for further application by integrating with a landscape dynamics model, representing the future challenge for the use of IBMs for tiger conservation.

Finally, this study addressed a very basic question with regards to the conservation of endangered species, about when and how extinction will occur in the future. The use of a different measure of time to extinction provides hints for answering when extinction will happen in the future. In particular, the use of the intrinsic mean time to extinction has improved the use of mean and median arithmetic time to extinction (Grimm and Wissel, 2004) as performed in Section 4.4, which not only provided a robust measure, it also recognized "quasi-extinction" which is determined by extinction of any sex class. This provides a careful and useful approach for the conservation of an endangered species, particularly for Sumatran tigers. Scenarios from different behaviour mechanisms of tigers and prey were tested in this study. The results from these tests address the "how question" for the extinction of tigers. Section 4.4 clearly showed that a simple adaptation in tiger feeding behaviour results in different extinction risks.

Chapter 6

Conclusions and Perspectives

6.1 Conclusions

The construction and the analysis of the Panthera Population Persistence (PPP) provides proper theoretical and application frameworks for the conservation of the Sumatran tiger population in central Sumatra. The PPP model was developed to gain insight into tiger-prey-habitat relationships as well as into the effect that human interferences and habitat configuration has on the persistence of tiger populations. The model addressed three main problems in the conservation of the Sumatran tiger: tiger poaching, prey depletion and habitat loss. This is reflected in four sub-questions in this dissertation.

1. *How does the relative importance of tiger poaching, prey depletion, and a combination of these factors affect on the probability of Sumatran tiger extinction*?

   Tiger poaching is the strongest predictor among other types of poaching for the Sumatran tiger's probability of extinction. The frequency of poaching is the most important poaching parameter that strongly affects Sumatran tiger population persistence. Thus, population viability analyses for this sub-tiger species should consider tiger poaching and the frequency of poaching, which was introduced into model for a better prediction of population dynamics.

2. *Does the anti-poaching program reduce the extinction probability of the Sumatran tiger population following poaching pressures*?

   The anti-poaching program was able to reduce the Sumatran tiger's extinction probability from the effects of prey depletion and a combination of tiger poaching and prey depletion, but was not able to compensate for tiger poaching. The ability of anti-poaching units to reduce the extinction probability depends on the type and parameters of the trap which represents poaching. Key points for successful conservation in the presence of poaching are the ability of anti-poaching units to detect the occurrence of poaching and to avert poaching.

3. *Do existing landscape configurations play a role in the extinction of the Sumatran tiger*?

   Landscape configuration near protected areas plays important roles in the persistence of the Sumatran tiger. However, existing landscape configurations could not support tiger conservation due to the relative low size of natural habitat.

4. *What is the best landscape configuration for sustaining tigers population in Central Sumatra* ?

   The best landscape configuration near a protected area is a logging concession. However, due to recent conditions in Sumatra, the agroforestry system should be established near protected areas and at the same time, be combined with eliminating the effect of tiger poaching.

6.2 Perspectives for Future Research

1. The PPP model has been used to explore the predator-prey-habitat relationship. The tiger's perceptual distance on the presence of prey is one important parameter which still needs to be observed in the field. Empirical studies on this parameter will be a novel finding for tiger ecology and should then be incorporated into the PPP model.

In addition, further studies about the comparison of perceptual distance from different predator-prey systems will provide a unified theoretical foundation for modelling this system.

2. Field observations of tiger and prey movement in relation to different habitat qualities and landscape configurations will provide an important contribution for the improvement of the PPP model to test the mechanism of response to different species on the presence of different habitat types and landscape configuration

3. The perception of a species on the presence of a given habitat differs in comparison to other species. Particular attention should be placed on the ability of each species to percieve habitat barriers and qualities in the landscape, such as the presence of riverine areas, main roads, and human densities. Thus, the representation of the landscape using a habitat suitability index map, which considers the effect of those barriers for each species modelled in the PPP model, might improve the predictive acuracy of this model.

4. The PPP model has not yet integrated the simulated tiger population to other populations in a larger geographical range. Integration with neighbouring populations will allow for the simulation of four main important processes in population dynamics: birth, mortality, immigration, and emigration. This integration will improve the ability of the PPP model to predict population consequences caused by individual behaviours.

5. In the conservation of highly threatened species like tigers, investigating whether the population still has the probability of survival and defining suggested conservation action that will help to avoid 100% extinction, which is referred as survival threshold, might provide a realistic solution. This measure is an optimistic way, which is the opposite point of view than looking for "probability of extinction". The improvement of the measurement of the survival threshold for a

structured population as simulated by the PPP model will provide a meaningful approach for assessing large-bodied predator populations under pressures from many factors as a result of human development.

6. One of the most important considerations for the majority of endangered species conservation is the long-term persistence of the given species, concerning their genetic diversity within and among populations. The PPP model will provide additional benefit for tiger conservation if this model is also used to simulate the effect of existing threats for the Sumatran tiger on the genetics flow among sub-populations.

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Appendices

Appendix A. The PPP Model Description

- **Purpose**
  The specific purpose of the PPP model is to investigate the potential mechanisms of tiger population dynamics under different environmental and management options. The simulated area of the PPP model is the Tesso Nilo National Park and its surrounding landscapeThe model was implemented in NETLOGO v. 4.1. (Wilensky, 1999).

- **Process Overview and Scheduling**
  The overall behaviour of tigers in the PPP model includes ageing, movement, hunger and starvation, hunting, feeding, reproduction, mortality and dispersal. The ageing process simply simulates increasing age in increment of 0.5 days, similar to the time step of the model. The age of an individual then determines its different behaviour according to its internal state. Figure .1 shows the behaviour of tigers in different age classes within the PPP model. Movements in the PPP are defined as random movement and directed movement.

  The PPP model simulates an increase in the hunger level of individuals by 10 for sub-adults and adults, 12.5 for females with cubs and no hunger behaviour for cubs. If an individual reaches its hunger level of 90, this is the onset of starvation behaviour leading to natural mortality when the starvation level reaches 30 after 60 days. Feeding behaviour resets the starvation level into zero and reduces the hunger level by 12.5 per time step during feeding. The hunting behaviour of a tiger is driven by its hunger level. A tiger is able to sense a prey within a certain hunting radius. Hunting success is assumed to be 50% on any hunting occasion (Sunquist, 2010), and tigers have a preference for killing Sambar deer (Reddy et al., 2004). If Sambar deer is absent from the model, then the tiger will only kills available prey.

  The PPP model simulates the reproduction of tigers through three

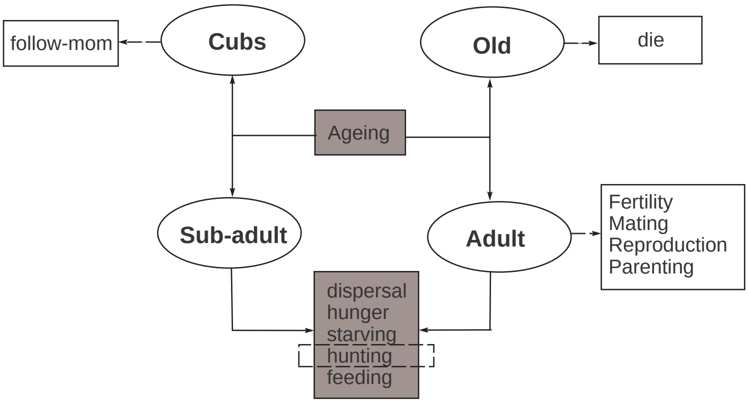

Figure .1: The flow-chart diagram of a tiger's basic behaviour in different age classes. Grey boxes show behaviour common to different age classes while empty boxes display behaviours that is particular for specific age class. The dotted box ilustrates the hunting behaviour which is similar to the NFM.

processes: fertility scheduling, mating, pregnancy and giving birth. A female reaches sexual maturity at the age of 825 days (Sunquist, 1981). In this case fertility scheduling is initiated. The inter-estrous interval of a female tiger is around 25 days during which the female is fertile for about 5 days. A fertile female will call to an adult male for mating. However, mating will only occur when hunger levels of individuals are lower than 60 and there is no starvation. Mating lasts for two days (Sunquist, 1981) and the female will have a 50% chance of becoming pregnant. The gestation period for a female is 102-103 days (Ahearn et al., 2001; Sunquist, 1981; Sunquist et al., 1999). A pregnant female has a random probability of giving birth to 1-3 cubs with a ratio of males to females of 1:3. A newborn tiger will usually adopt all characteristics from its mother except for its sex class, age, its hunger level and its starvation level. The age of cubs is set as 0 at the time step of birth. The hunger and starvation levels are also set as 0 until the cubs reach sub-adulthood. A female with cubs will not display any mating behaviour until the cubs reach sub-adult classes. Density dependent birth rate for both Red Muntjac and Sambar deer are simulated. At the sub-adult level, tigers search for a home range. The home range of a male might overlap with that of one or several females but never with the home range of another male. An adult individual without a home range is removed from the model but is not considered as a dead individual. The PPP model calculates this as a dispersed individual.

- **Design concept**

  The dynamics of the tiger population are expected to emerge from the interaction between tiger individuals, prey and habitat. The PPP model explicitly simulates four types of interaction. The first is a prey-habitat interaction, which shows the movement and the foraging behaviour of prey in different habitat types. The prey decides whether to move to the next patch or to stay depending on certain habitat indices. Such indices also determine the energy gained by the prey while foraging. The second type of interaction is a tiger-prey interaction, which represents the behaviour of a tiger hunting prey. The third type of interaction is tiger-prey-habitat, which represents the time taken to consume prey that has been killed in different land-use types. The fourth type is a tiger-tiger interaction, which simulates the behaviour of mating and parental care (between a mother and her cubs).

  A tiger prefers to kill large prey. However, when there is no large prey in the hunting radius, the tiger will automatically search for small prey. Newborn tigers inherit this preference for large prey. Adult tigers are known to compete for resources and mating (Sunquist, 1981). When an adult individual cannot establish a home range, the model considers it as transient and omits it from the landscape. Tigers are able to detect both prey and a mate, and a cub senses the presence of its mother to be followed. Stochasticity is applied to the probability of a tiger to successfully hunt for prey, the probability of becoming pregnant, the number of new cubs and the proportion of male and female cubs. Collectiveness occurs during mating and parenting behaviour. A male and a female will remain together over the mating period, and a female will stay with its cubs until they reach the sub-adult class.

- **Details**
  Initialization An adult male Sumatran tiger requires 116 km^2 to maintain a home-range, and 70 km^2 for a adult female (Franklin et al., 1999). We set the population to 20 sub-adult tigers with 10 males and 10 females. The densities of Red Muntjac and Sambar deer in tropical forest were set according to the findings of O'Brien et al. (O'Brien et al., 2003). Sambar deer has a density range of 0.88 - 1.42 individuals /ha whereas Red Muntjac has a range of 3.96- 4.44 individuals/ha. The model has 203 x 149 grid cells, representing the Tesso Nilo National Park and its surrounding land-use. Each grid cell represents 12.7 hectares and is specified by habitat quality, corresponding to the land-use types.

  Submodels We included four main types of prey behaviour: movement, foraging, reproduction and mortality. Prey movement is defined by two main factors: direction and distance. The distance refers to data obtained for red deer movement Fryxell et al. (2008) which varies from 0.23 - 7 km/day. The direction of movement is driven by habitat quality indices. The probability of prey movement is calculated as follows:

  $\alpha = \beta 1/(\beta 1 + \beta 0)$

  with α being the movement probability to the next patch, $\beta 1$ being the habitat index of the next path and $\beta 0$ being the habitat index of the current patch. If a $\alpha < 0.5$ then the prey will stay in the current patch, otherwise it will move to the next patch. We did not differentiate between the distance and direction for Sambar deer and Red Muntjac.

  Prey will remain in a patch and consume a certain amount of the food resource in that particular patch. Prey receives different resource values in different land-use types. At the same rate of increased hunger level, the greater the human intervention, the less the energy that is gained from the patch, and consequently the more easily the prey becomes hungry. Both Red Muntjac and Sambar deer increase their hunger level by 10 levels per time step. Since we do not have any data on the rate of consumption of prey species within different habitat types, we used the same rate for all types of habitats. Red Muntjac start to reproduce annually from the age of 2 to 4 years with probability of a number of litters consisting of 3 individuals. Sambar deer reproduce annually with 1 litter from the age of 2 years to 6 years. Both prey die when they reach a maximum age (approx. 10 years for Red Muntjac and 17 years for Sambar deer), from acute starving (hunger level is greater than 200), and/or are killed by tigers. Both Sambar deer and Red Muntjac have density-dependent birth rates. Both will continue to reproduce until the population reaches the carrying capacity.

Appendix B. Description of Notonecta Foraging Model (NFM)

- **Purpose**
  The Notonecta model was designed to predict the functional responses of juvenile Notonecta maculata foraging on Daphnia magna. Moreover it was intended to assess whether the combination of foraging elements selected (encounter distance, attack rate, success rate and handling time) account for the size selectivity observed in laboratory studies. The model is implemented in Delphi® using Borland Delphi® 2007 for the Win32® Professional Edition.

- **States variables and scales**
  The model is arranged in three hierarchical levels: the ecosystem, the population, and the individuals. The ecosystem level features the light regime (light/dark) and the volume of the test vessel at the laboratory scale. The state of the daphnid population is defined as the abundance of Daphnia magna which is allowed to change due to backswimmer predation only whereas the Notonecta maculata population is restricted to a single backswimmer in the current state of the model. Individual backswimmers and individual daphnids are characterized by a set of state variables at the start of the simulation. Properties of D. magna are the identification number and size. Backswimmer properties are instar, encounter distance, handling time as well as attack-and-success coefficients. Attack rate, success rate and handling time depend on the size of the prey item encountered.

- **Process overview and scheduling**
  The model proceeds in discrete time steps in seconds. It follows a general predation cycle divided into four stages: (1) A prey item is randomly chosen and the time until an encounter is calculated. The probability of (2) attack and (3) capture success is calculated for the prey item selected. In case of capture success handling time is calculated and the prey item eaten is removed from the population (4).

- **Design concepts**
  Population size of Daphnia depends on the foraging of individual Notonecta. However, population dynamics do not emerge from any individual properties. An adaption or fitness seeking is not explicitly modelled, but is included in the empirical submodels. Environmental and population level factors sensed by Notonecta are the light regime and the daphnid prey. The interaction between individual Notonecta and Daphnia is feeding. The body length of Daphnia is stochastically selected from a normal distribution. Variations in attack rates and success rates of Notonecta are generated by a normal distribution with the mean of 1 and a coefficient of variation resulting in an individual parameter multiplied by the mean rate calculated from submodels. The decision whether to attack, or whether the attack is successful, is based on two random numbers between 0 and 1 selected in every encounter. In case the calculated rate exceeding the random number the attack or the success is rejected. Handling time is calculated for every daphnid cough, using a normal distribution.

- **Details**

  The initialisation of settings comprises the Notonecta instar and Daphnia sizes, the volume of the environment, prey abundances tested, simulation time and the number of Monte-Carlo runs. Sensitivity analyses of single parameters were carried out using a single backswimmer foraging on 100 prey items, 0.6 - 3.7 mm in size, in a 1l environment for three hours, running 1000 Monte-Carlo simulations. No additional input is necessary for the simulation. Equations and parameters of submodels described below were derived empirically from laboratory experiments. The time until an encounter (te) between predator and prey is calculated based on the predators encounter volume and an encounter probability depending on the prey size (s) and density, i.e. the ratio of the prey number (nd) and the volume of the environment (v). The encounter volume is assumed to be a hemisphere where the radius equals the backswimmers encounter distance (de). Time until encounter is given by:

$$te = (2.095\ de^3\ v)/((0.35\ s + 0.34)(0.006\ nd^2 + 0.12\ nd))$$

The attack rate (Ar) was observed to depend on prey size (s) and is calculated by means of a lognormal function where Aa, Ab, Ax0 and Ayo are instar specific parameters listed:

$$Ar = (Ay0 + Aa\ \exp(-0.5\ \ln(s\ Ax0\ /\ Ab)))/100$$

Here, the success rate (Sr) is calculated in the same manner using the parameters Sa, Sb, Sx0 and Sy0. The handling time (th), i.e. the time from the actual attack until the release of daphnid remains is calculated by means of a linear regression of Daphnia size (s) and log transformed handling time data, using the instar specific parameters Ha and Hb and a proportionality factor $\tau = 1[s]$:

$$th = 10^{Has+Hb}\ \tau$$

Appendix C. Description of parameters in the PPP model

Parameter name	Description	Units	Note
A_{mat}	Maturity age	825 days	(Sunquist et al., 1999)
C_m	Initial density for Red Muntjac	2.2 ind/km^2	(O'Brien et al., 2003)
C_s	Initial density for Sambar deer	1.4 ind/km^2	(O'Brien et al., 2003)
G_m	Growth rate of Red Muntjac	2-3 ind/km^2	(Chapman et al., 1997)
G_s	Growth rate of Sambar deer	1 ind/km^2	(Semiadi et al., 1994)
H_{fem}	Female Home-range	70km^2	(Franklin et al., 1999)
H_{male}	Male Home-range	116km^2	(Franklin et al., 1999)
Ht_{rad}	Hunting radius of tigers to detect the presence of prey	1,000 m^2	Adjusted
P_c	Probability of successfull hunting	50 %	(Sunquist, 2010)
P_{preg}	Probability to pregnant	50 %	Adjusted
T_{fer}	Time duration to switch fertility status	25 days	(Sunquist, 1981)
T_{fm}	Time duration to feed Red Muntjac	1-3 days	(Sunquist, 1981; Sunquist et al., 1999)
T_{fol}	Time duration for cubs to follow their mother	660 days	(Sunquist, 1981)
T_{fs}	Time duration to feed Sambar deer	7 days	(Sunquist, 1981; Sunquist et al., 1999)
T_{mate}	Time duration for mating	2 days	(Sunquist, 1981; Sunquist et al., 1999)
$\mu\ feed$	Mean rate of movement distance and direction during feeding	400 m/day	(Ahearn et al., 2001)
$\mu\ fer$	Mean rate of movement distance and direction during fertile	1,000 m/day	(Ahearn et al., 2001)
$\mu\ hunt$	Mean rate of movement distance and direction during hunting movement	1,000 m/day	(Ahearn et al., 2001)
$\mu\ mat$	Mean rate of movement distance and direction during mating	3,000 m/day	(Ahearn et al., 2001)
$\mu\ par$	Mean rate of movement distance and direction during parenting	1,500 m/day	(Ahearn et al., 2001)
$\mu\ preg$	Mean rate of movement distance and direction during pregnancy	2,000 m/day	(Ahearn et al., 2001)
$\mu\ rand$	Mean rate of movement distance and direction during random movement	2,000 m/day	(Ahearn et al., 2001)
$\sigma\ feed$	Standard deviation of movement distance and direction during feeding	400 m/day	(Ahearn et al., 2001)
$\sigma\ fer$	Standard deviation of movement distance and direction during fertile	1,000 m/day	(Ahearn et al., 2001)
$\sigma\ hunt$	Standard deviation of movement distance and direction during hunting movement	1,500 m/day	(Ahearn et al., 2001)
$\sigma\ mat$	Standard deviation of movement distance and direction during mating	1,000 m/day	(Ahearn et al., 2001)
$\sigma\ par$	Standard deviation of movement distance and direction during parenting	800 m/day	(Ahearn et al., 2001)
$\sigma\ preg$	Standard deviation of movement distance and direction during pregnancy	1,000 m/day	(Ahearn et al., 2001)
$\sigma\ rand$	Standard deviation of movement distance and direction during random movement	2,000 m/day	(Ahearn et al., 2001)

Erklärung

Hiermit versichere ich, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe; die aus fremden Quellen direkt oder indirekt übernommenen Gedanken sind als diese kenntlich gemacht worden.

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Ich bestätige, dass ich die Promotionsordnung der Fakultät Forst-, Geo- und Hydrowissenschaften der Technischen Universität Dresden anerkenne.

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