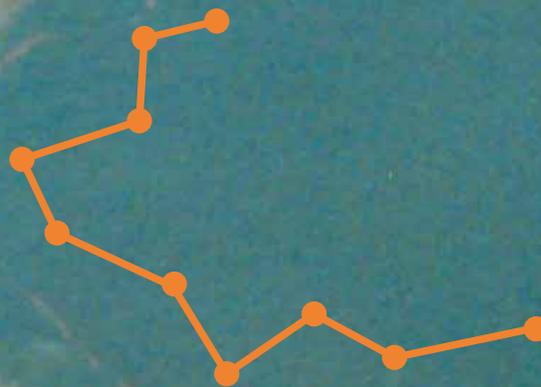


# Seasonality in spatio-temporal behaviour of female orangutans

A case study in Tuanan Mawas,  
Central Kalimantan, Indonesia



Master thesis by  
Flurina Wartmann

University of Zurich

# **Seasonality in spatio-temporal behaviour of female orangutans**

**A case study in Tuanan Mawas,  
Central Kalimantan, Indonesia**

**Supervised by:**

**Dr. Ross S. Purves  
Geographical Institute  
University of Zurich  
Switzerland**

**Prof. Dr. Carel P. van Schaik  
Anthropological Institute and Museum  
University of Zurich  
Switzerland**

**Faculty member:**

**Prof. Dr. Robert Weibel  
Geographical Institute  
University of Zurich  
Switzerland**

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**Flurina Wartmann  
Sonnenbergstrasse 33  
CH- 8102 Oberengstringen  
flurina.wartmann@access.uzh.ch**

## Summary

Although the seasonal temperature variation in regions close to the equator is limited, tropical habitats are subjected to fluctuations in rainfall and abundance of vegetation. Therefore, the abundance of food available for primary consumers also varies. Primates can respond to fluctuating fruit availability by changing their diet or ranging behaviour (e.g. by increasing or decreasing ranges). Previous studies have shown that Sumatran orangutans (*Pongo abelii*) exhibit seasonal ranging patterns that are linked to important fruiting events (mast fruiting). However, less was known on the seasonality of ranging patterns of Bornean orangutans (*Pongo pygmaeus wurmbii*). The key questions in this study thus were how female orangutans react to seasonal changes in their environment and how these responses in spatio-temporal behaviour can be effectively modelled and analysed.

Animal ranging can be modelled using the concept of home ranges. However, there are a lot of issues involved when applying home range models to analyse animal space use and so far there is no consensus in the scientific community on which model is best to be applied.

Therefore, the methodological part of this study aimed at finding a model that was suited for the specific data set. Furthermore, the effect of several uncertainties in the model such as data, parameter selection and sample size on range estimates was analysed. Based on these analyses a procedure to calculate home ranges was arrived at which is objective, reproducible and based on real movement data. Consequently it was ensured that the ranging analyses are meaningful and not based on methodological errors.

A key point of this study was to apply these spatio-temporal models to analyse the seasonal movements of orangutans. As orangutans primarily feed on fruit when it is abundant, seasons were divided according to fruit availability. Orangutan females occupied the same areas for several years. No seasonal effect on range sizes for individuals was found. A marked difference in feeding behaviour and daily path length was found between seasons of high and low fruit availability: When fruit was scarce, orangutans foraged more on vegetative matter and travelled shorter distances. On the other hand when fruit was abundant, they significantly increased travel distances. Orangutan females thus do show seasonal changes in their feeding and ranging behaviour. However, those responses are not reflected in range size, but in the manner *how* the range is used.

## Zusammenfassung

In Regionen nahe dem Äquator weisen die Temperaturen kaum saisonale Schwankungen auf. Trotzdem treten auch in tropischen Habitaten saisonale Veränderungen auf, die sich in der Regenmenge und Üppigkeit der Vegetation äussern. Dadurch verändert sich aber auch die Verfügbarkeit von Nahrung für Pflanzenfresser. Primaten können auf Fluktuationen in der Verfügbarkeit von Früchten auf verschiedene Arten reagieren, zum Beispiel indem sie ihre Streifgebiete vergrössern oder verkleinern. Frühere Studien haben gezeigt, dass die Bewegungsmuster von Orang-Utans auf Sumatra (*Pongo abelii*) stark saisonal variieren in Abhängigkeit des Vorhandenseins von Früchten. Bis jetzt war aber relativ wenig über das saisonale Bewegungsverhalten von Orang-Utans auf Borneo (*Pongo pygmaeus wurmbii*) bekannt. Die Schlüsselfragen dieser Arbeit waren, wie weibliche Orang-Utans auf saisonale Schwankungen der Umweltbedingungen reagieren und wie diese Reaktionen des raum-zeitlichen Verhaltens modelliert und analysiert werden können.

Tierbewegungen können mit dem Konzept der „home ranges“ abgebildet werden. Wenn diese Modelle unkritisch angewendet werden, können allerdings Probleme entstehen. Ausserdem besteht bis jetzt in der Wissenschaft keine Einigkeit darüber, welches Modell am besten geeignet sei, um die Raumnutzung von Tieren abzubilden.

Deshalb befasst sich der methodische Teil dieser Arbeit damit, ein Modell zu finden, welches für die vorliegenden Daten am besten geeignet ist. Ausserdem wurde der Effekt von Unsicherheiten im Modell, so etwa die zu Grunde liegenden Daten, die Parameterwahl und die Stichprobengrösse auf die Modellresultate untersucht. Basierend auf diesen Analysen wurde eine Methode ausgewählt, die objektiv und reproduzierbar ist und zudem auf realen Daten beruht. So konnte sichergestellt werden, dass die Analyse des Bewegungsverhaltens sinnvolle Resultate liefert, die nicht auf methodischen Fehlern basieren.

Ein Schwerpunkt dieser Arbeit lag darin, diese Raum-Zeit-Modelle anzuwenden, um das saisonale Bewegungsverhalten von weiblichen Orang-Utans abzubilden. Da Orang-Utans sich hauptsächlich von Früchten ernähren, wenn diese verfügbar sind, wurde die Einteilung der Saisonalität anhand eines botanischen Frucht-Verfügbarkeits-Indexes vorgenommen.

Die Resultate zeigen, dass Orang-Utan-Weibchen sich während mehreren Jahren in denselben Gebieten aufhalten. Die Grösse der genutzten Gebiete zeigt keine saisonale Schwankung. Hingegen wurden Unterschiede im Fressverhalten sowie in der Länge der täglich zurückgelegten Wegdistanzen gefunden: Wenn wenig Früchte verfügbar waren, wurde mehr Zeit darauf verwendet, vegetatives Material wie Blätter zu fressen. Ausserdem legten die Orang-Utan-Weibchen pro Tag kürzere Wegstrecken zurück. Waren hingegen viele Früchte vorhanden, legten die Orang-Utans signifikant längere Wegstrecken zurück. Orang-Utan-Weibchen zeigen demnach saisonale Unterschiede in ihrem Fress- und Bewegungsverhalten. Die Unterschiede liegen jedoch nicht in der Grösse der verwendeten Gebiete, sondern in der Art und Weise, wie diese Gebiete genutzt werden.

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# 1. General introduction

Geographic Information Systems (GIS) have experienced a rapid expansion over the last few years. With their scope of analytical tools and their integration into wildlife biology they have improved our ability to study and understand wildlife movement patterns. This study aims at combining the field of Geographic Information Systems with primatological research to model and analyse space-use patterns of wild orangutans. The key questions in this study were how orangutans react to seasonal changes in their environment and how these responses in spatio-temporal behaviour can be analysed.

Seasonal variation of temperatures in the tropics is limited, as the daily variation exceeds the variation in monthly means. However, seasonal variation in rainfall and sunshine characterizes all tropical habitats. Although animals may respond directly to weather, the main impact of climatic seasonality is indirect. Climate has a fundamental effect on vegetation and therefore on the abundance and distribution of potential food items. Most primates preferably exploit ripe fruit when it is available (van Schaik & Brockman 2005: 3-5). Fruit availability was reported to be related to seasonal climatic patterns and to fluctuate annually.

In addition to annual peaks in fruit production, supra-annual mast-fruiting events occur in Southeast Asian rain forests. Mast fruiting is a phenomenon in which the dominant dipterocarp trees fruit in synchrony after years of reproductive inactivity (Knott 1998: 1062). The phenomenon occurs in periods of approximately every 2 - 7 years and is linked to the El-Niño Southern Oscillation (ENSO) events (Salafsky 1994: 373). ENSO events are caused by irregular warming of sea temperatures in the eastern pacific which lead to weather anomalies such as periods of long droughts in Southeast Asia (van Schaik & Pfannes 2005: 26). Particular ENSO events were found to be distinctly associated with droughts in Java (Harger 1995: 1946) and the intensity of these ENSO linked dry periods was demonstrated to have been increasing over the past two or three decades (Salafsky 1994: 373).

Due to both the within-year and between-year variation in food availability, primary consumers were forced to adapt to changes in resource abundance. The periodicity of food scarcity has supposedly led to the evolution of a wide range of morphological, physiological and behavioural adaptations in primary consumers (van Schaik et al. 1993: 368), including primates.

Primates can respond to food scarcity or abundance by changing their diet or ranging behaviour (e.g. by increasing or decreasing home range) and by switching habitats (Brockman & van Schaik 2005: 6). As a recent phenomenon, anthropogenic influences have become superimposed on the natural cycles of seasonality in the tropics (Walther et al. 2002: 389). Global climatic change will also affect tropical rainforests and the species living therein. One example is the orangutan, a great-ape species inhabiting the remaining forests on the

islands of Borneo and the northern parts of Sumatra. Orangutan numbers have been declining over the past few years, mainly due to habitat loss and fragmentation caused by logging activities (Felton 2003: 91). Several populations remain in legally protected areas such as national parks or protected areas like the Tuanan Mawas reserve in Central Kalimantan. While orangutan habitats and populations are getting smaller and smaller, it is vital to improve our understanding of orangutan space use and ranging behaviour. Analysis of spatio-temporal behaviour of orangutans helps us understand how these animals respond to seasonality in their environment and could ultimately contribute to the conservation of this endangered species.

Orangutan range use of the Sumatran species (*Pongo abelii*) has been studied in detail by Singleton & van Schaik (2000). They showed that ranging behaviour was linked to seasonal patterns and mast fruiting events. Orangutans used the altitudinal range to follow fruiting peaks; their home ranges included a variety of habitats from lowland peat swamp forest to hill forests. However, there is still relatively little known on the seasonal range use of the Bornean orangutan (*Pongo pygmaeus*) in the peat swamp forests of Kalimantan. A preliminary study was conducted in Tuanan (Petterson 2007, unpublished) where annual home ranges were estimated. This study showed that home ranges of Bornean orangutans were smaller than their Sumatran relatives. The reason for this difference remains yet to be investigated in detail. However, when annual home ranges are used to estimate the animal's space use, important details of range use will be lost, such as seasonally more intensively used patches where fruiting occurs.



Fig. 1 Map of field sites in Sumatra and Borneo (<http://www.aim.uzh.ch/orangutanetwork/FieldsiteList/Map.html>)

The key question of this research is how seasonal environmental changes in climate, vegetation and food abundance influence ranging behaviour of this particular orangutan

population and how these changes can be effectively modelled and analysed. Of special interest was how different uncertainties in the data as well as in the models influence ranging estimates.

Animal space use can be modelled using the concept of home ranges. However, there are a lot of issues involved when applying home range models to analyse ranging and so far there is no consensus in the scientific community on which model is best to be applied. The simple geometric definition of home ranges called “Minimum convex polygon” (MCP) method was long favoured among wildlife biologists (Worton 1995). The more recent approach of kernel density estimations uses a probabilistic method of defining animal space use and is now increasingly being used among wildlife biologists (Börger et al. 2006: 1394). Because models perform differently for different data sets, the model needs to be selected according to objective criteria. The “information-theoretic approach” (Horne 2006a) was developed as a theoretical approach for home range model selection and can be applied to compare different models and select the best home range model for a specific data set. Furthermore, attention needs to be paid to underlying uncertainties such as measurement error and to other influential factors like sample size that could affect model results.

Another approach to investigating space use is to apply the geospatial lifeline concept (Laube et al. 2007) to orangutan travel routes. By linking spatial information on travel routes with behavioural data of feeding time for the same day, orangutan responses to seasonality can be analysed from different perspectives.

The study comprises two major aspects: One goal is to select the model best suited for the data and to investigate the influence of factors such model and sample size on results. The second goal is to apply these techniques of spatio-temporal data analysis to investigate seasonality in space-use of orangutans. The main research questions were:

- *What uncertainties are associated with the data and models used to estimate ranges and how do they influence model results?*
- *How do seasonal environmental changes in food abundance influence ranging behaviour of female orangutans?*

The study postulates two main hypotheses:

1. Estimations of home range differ significantly between methods and sample sizes used
2. Spatio-temporal behaviour of orangutan differs significantly between the fruiting seasons

## 1.1 Study site

The Tuanan field station is located in the Mawas reserve in Central Kalimantan, Indonesia (2.151° South; 114.374° East) and lies about 2 kilometres from the Kapuas river. Altitude above sea level is approximately 40m and the surrounding landscape is completely flat. The research area lies within a heavily logged secondary peat swamp forest (see figure 2).



Fig. 2 Secondary peat swamp forest and boardwalk

Through selective logging in the early 1990s, followed by informal logging, the forest has been heavily disturbed (van Schaik, pers. comm. 2007). A local non-governmental organisation protected the area to allow natural regeneration of the forest. Orangutans living in the Tuanan Mawas reserve were not released from captivity but are wild animals (with perhaps a few animals having immigrated from recently destroyed habitat along the edges). Research on orangutans started in January 2003, data collection on weather and phenology started later the same year and both are still ongoing. A grid-based trail system of manually cut transects encompasses an area of about 750ha, constituting the study site.

Three major boardwalks of approximately 6km cross the study site from East to West and from North to South respectively. Transects are tagged every 50 meters and all intersections are labelled, making localisation near transects and intersections easy. The trail system was recently expanded both in the East and North-Western part of the study site.

## 1.2 Climate and phenology at the study site

The Tuanan research station lies 2 degrees south of the equator. Typical for a tropical region, it is a year-round hot and humid climate with the diurnal temperature variation being greater than the seasonal variation. Variability in temperatures is small. The average maximum temperature from beginning of observations in 2003 to end of 2007 was 29.15°C. The average minimum temperature for the same period was 22.93°C. Thus, the most relevant seasonal variation in the tropics is found in rainfall and irradiance (van Schaik & Pfannes 2005: 24). Variability in irradiance is more difficult to measure than rainfall. Therefore the latter is usually relied on to characterize both, which in many cases is acceptable due to the relationship of rain and clouds (van Schaik & Pfannes 2005: 36). In Tuanan, mean rainfall per year from 2004 to 2007 was 2678 mm, and average monthly rainfall was 223.23 mm. Minimum monthly rainfall was 0 mm in August and September 2004. The maximum total rainfall per month of 717 mm was recorded in March 2005 (figure 3).

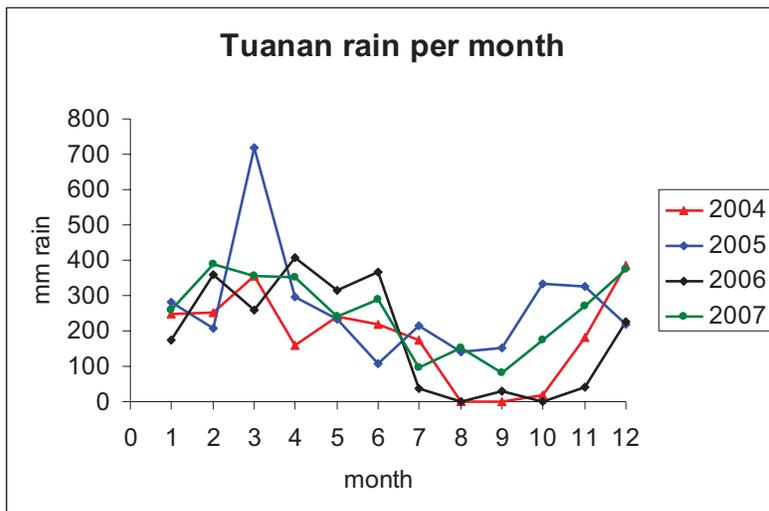


Fig. 3 Monthly rainfall for the years 2004 – 2007 at the Tuanan field station

Two seasons occur per year. The dry season usually lasts from June until October; the onset of the wet season is usually between October and December (Haag 2007: 13). Variation in climatic conditions is linked to vegetation patterns and food availability for orangutans. The production of flowers shows a seasonal pattern with a flowering peak from September to October during the late dry season. Fruits peak approximately 3 months after the flowers. Fruit abundance thus shows a peak during the wet season (Haag 2007: 15). Orangutans are a primarily frugivorous species and prefer fruits when they are abundant, which is reflected in time spent feeding on those food items. Haag (2007: 36) found in her study that orangutans in Tuanan spend most of their total feeding time feeding on fruits (67%) and that 13-90% of their diet consists of fruits. Therefore, availability of their preferred food items rather than temperature or rainfall is likely to influence ranging patterns of orangutans.

### 1.3 Orangutans - A glimpse into behavioural ecology

In the wild, orangutans are found on two islands: Borneo and Sumatra. Although they are closely related, the populations on the two islands are now commonly regarded as two species: The Bornean orangutan (*Pongo pygmaeus*) with three subspecies (*Pongo pygmaeus wurmbii*, *Pongo pygmaeus pygmaeus* and *Pongo pygmaeus morio*) and the Sumatran orangutan (*Pongo abelii*). Their main habitat is primary rainforest, but nowadays this type of habitat is becoming rare, giving way to disturbed forests where timber is commercially or informally extracted. Although orangutans can survive in partially logged forests, it has been suggested that this disturbed environment negatively affects their health status and reproductive success (Felton et al. 2003: 99). Both species primarily feed on fruit when they are available, but also consume leaves, bark, flowers and insects. Requiring large amounts of calories, orangutans spend approximately half of their day feeding (Knott 1998). Orangutans are active only during the daytime. In the late afternoon, every adult builds a sleeping platform (nest) for the night within the crown of a tree, using small branches and leaves to make a platform. They are arboreal mammals, spending most of their lives in the tree canopy and only very rarely descend to the ground.

Orangutans usually give birth to only one infant at a time. Infants are entirely dependant on their mothers during the first two years of their life. Young orangutans are not fully weaned from milk until they are about 6 to 7 years old. By the age of 7 to 9, the mother will usually give birth to a new infant. At that age, the juveniles have learned the necessary skills from their mother to survive in the forest on their own and spend increasingly longer periods away from her.



Fig. 4 Infant orangutan Jerry and his mother Jinak (in the back)

Female orangutans reach sexual maturity at about 15 years of age. Males will become sexually mature at ages of 13 to 15. Sexually mature males can be divided into two groups: unflanged and flanged males, a phenomenon called “bimaturism”. Although sexually mature, not every male will grow the characteristic cheek pads called “flanges”. Flanged males are often the dominant male in an area and females prefer to mate with flanged males. Only flanged males are able to make the characteristic long calls that are hypothesized to serve both for attracting females and for warning other males.

Orangutans tend to be, apart from the mother-infant dyad, solitary animals, especially in Borneo. For most of the time, the male lives alone while the female cares for one young. The sexes meet for short periods to mate. These so called “consortships” can last for only some days in Borneo to several months in Sumatra. However, forced matings, often by unflanged males, are not uncommon among orangutans (Payne 2008: 12-15, Delgado & van Schaik 2000). In the wild, orangutan males can reach ages of at least 58 years and females of at least 53 years (Wich et al. 2004: 385).

## 2. Uncertainties in the data and in home range estimates

### 2.1 Introduction

It is important to understand the source of uncertainties in animal location data and the magnitude of these effects on inferences made from the data. This helps researchers to provide a more complete and unbiased picture of how an animal behaves in space and time (Whitey et al. 2001: 44-45). In the literature, two different measures of data quality are often intermingled: Precision and accuracy. Precision is a measure of the consistency of a measurement system, e.g. mapping or recording locations with GPS. It is often reported as the standard deviation of location errors. The problem is that in many studies precision is measured but then used to indicate accuracy. Accuracy is a measure of how close an estimated location is to the actual location (Whitey et al. 2001: 60-61). Although there are usually many uncertainties associated with field data, they are seldom reported in animal space use studies (Moser & Garton 2007: 2421). Whitey et al. (2001: 44-45) found that almost half of all radio telemetry papers published in the *“Journal of Wildlife Management”* inadequately reported location error or did not report it at all. In Tuanan, all data is currently collected manually by mapping and subsequent digitalization. An alternative would be the use of GPS technology. Those two methods differ in terms of accuracy and associated uncertainties.

A central question in ecology is how observed spatial patterns in the distribution of individual animals within populations are determined by the interactions between individuals and their environment. A useful approach is to understand the dynamics of animal movements in relation to social and ecological factors. As most animals use the same areas repeatedly over time, animal movements are often defined using the home range concept (Börger 2006: 1394). The home range of an animal can be vaguely referred to as its habitat. Following the definition of Burt (1943: 351), the home range was defined as *„that area traversed by the individual in its normal activities of food gathering, mating, and caring for young”*. Thus occasional excursions outside the area should not be considered part of the home range. Over time, the need for standardization and statistical analysis of home ranges has led to more explicit definitions. A quantitative definition of the home range is an animal's utilization distribution (UD). Van Winkle (1975, in: Seaman 1996: 2075) defined it as *“the two-dimensional relative frequency distribution for the points of location of an animal over a period of time”*. The utilization distribution is an estimate of the probability of the relative amount an animal spends at any place and can be used to predict where an animal occurred but was not observed (Horne 2006b: 641). Although the home range is a fundamental ecological concept for animal space use, there is a considerable debate in the literature on how it is best to be measured (Börger 2006: 1393). The number of methods used to estimate

home range size is large and increasing (Horne 2006a: 1146). However, choosing one method over the other is difficult because all have disadvantages and home-range size varies markedly according to the method chosen (Girard 2002: 1290), which introduces uncertainties into range estimates made by different models. Home range estimation methods have been reviewed by qualitatively comparing strengths and weaknesses or by assessing model fit with computer simulations (Horne & Garton 2006a: 1146). Known home ranges are generated and then the fit of various home range models to the simulated distribution is compared. Although this can be a powerful approach of evaluating home range models, Horne & Garton (2006a: 1146) point out that studies using computer simulations often show that how a home range model performs depends on the assumed distribution. This leads Börger et al. (2006: 1394) to state: *“Given these issues, it is surprising that few non-simulation-based studies have explored how home range estimation varies with method, sample size and sampling regime [...]”* Authors have also expressed concern on several methodical aspects and uncertainties of currently used home range models such as sample size and autocorrelation (Horne et al. 2007a: 996).

### **2.1.1 Uncertainties in the data**

For data that are collected by manual mapping of focal animals within sight, errors in the data will be entirely anthropogenic. As Whitey et al. (2001: 55) put it: *“Placing the location of an animal or an observer on a map is not necessarily a simple task”*. This can only be emphasized in the context of the peat swamp forest in Tuanan. Errors may arise if observers are uncertain about the location and have no means of checking their position (e.g. within transect-squares).

As opposed to manual mapping, the Global Positioning System (GPS) allows an automated collection of animal locations. Spatial inaccuracy is defined as the discrepancy between a location recorded by the GPS receiver and the true coordinates on the ground. Spatial accuracy of locations obtained with a GPS is a function of satellite configuration, satellite availability and habitat attributes such as canopy cover and terrain (Sager-Fradkin et al. 2007: 1298, Lewis et al. 2007, D'Eon et al. 2002, Di Orio et al. 2003). Cain et al. (2005: 931) conclude in their review on telemetry studies with GPS collars that most studies found characteristics of vegetation such as canopy cover, tree height, tree density and canopy type to have an influence on GPS location error. There seems to be a consensus in the literature that GPS location error varies due to several habitat characteristics. Canopy cover was identified as an important factor influencing GPS location error. Type of vegetation, season of the year (leaf-cover) and tree height were also named as influential factors (Cain et al. 2005).

After the procedure of introducing an artificial error in to signals was discontinued in the year 2000 it was reported that GPS receivers located 95% of locations within a radius of less

than 10m (Whitey et al. 2001: 102-103). Phillips et al. (1998) investigated acquisition rates in neotropical rainforests in Costa Rica and found a significant relationship of canopy cover measured with a densitometer and ability to obtain a position fix (Chi-square = 53.79,  $p < 0.0001$ ). As a conclusion they added: *“unless the acquisition rate can be enhanced, recreational GPS units may not be a practical tool for use in Neotropical forests”* (Phillips et al. 1998: 171). Since then, the GPS technology has been further developed and recreational devices are now also being used for scientific purposes. In their study in a relatively open terrain in Arizona (USA), with vegetation height smaller than 3 meters, Cain et al. (2005: 931) found the GPS location error to vary between 2 - 75 meters, the mean being 9.7 meters (standard deviation was not reported). Sager-Fradkin et al. (2007: 1203) conducted a study on GPS location error in coniferous forests in Washington (USA). Locations estimated based on 3 satellites (2-dimensional) had an average location error of 62.6 meters. Of the 3-dimensional fixed, 95% were in the range of 17.7 meters.

In Tuanan, GPS location error was reported by field researchers to be a problem for data collection (Lynda Dunkel 2007, pers. comm.). Often no position could be obtained during the afternoon. This might be due to an interaction of satellite availability and canopy cover. Therefore it is important to assess signal accuracy and determine factors influencing GPS signal precision at a specific study site. This is also relevant for future studies because researchers want to know whether data collection by hand-held GPS receivers is accurate for later analysis. The key questions that the field research addressed were:

- *How large are location errors associated with follow maps?*
- *How large is the GPS location error at the Tuanan field station?*
- *Which method of field data collection performs better?*

The hypothesis was that because of the trail density manual maps are accurate up to approximately 30 metres and that maps drawn from GPS data are more accurate. Furthermore it was hypothesized that GPS signal accuracy would be negatively influenced by canopy cover.

### **2.1.2 Uncertainties in home range estimates**

In this study the following questions were addressed for a real spatio-temporal data set of orangutans:

- *How do home range size estimates vary with method and sample size?*
- *What influence does method and different parameters have on home range estimates?*
- *Which method should be chosen and why?*
- *How can the model and parameter selection be optimized using objective criteria?*

Of further interest were the influence of observation bias and the conversely discussed issue of the importance of spatial and temporal autocorrelation. The question addressed was:

- *Is autocorrelation a problem in home range size estimates and if yes, how can it be dealt with?*

Börger et al. (2006: 1401) showed in their study that most of the variation in home range sizes can be accounted for by differences among individuals and study sites regardless of estimation method used. This assumption was tested for orangutan data in order to confirm that results from comparison of home ranges between individuals will be meaningful. It was hypothesized that the different models, sample sizes and parameters used will all significantly influence the estimates of home range sizes.

## **2.2 Theoretic background**

The following sections give an overview on the theory of home range estimations used. For a more thorough introduction please refer to Millsaugh & Marzluff (2001).

### **2.2.1 Minimum Convex Polygon**

The MCP is an example of a method that geometrically defines the home range as the convex hull around a set of point locations. In the past, the MCP method has enjoyed popularity in home range modelling due to the simplicity of the concept and its easy implementation. However, using the MCP method for home range modelling has been heavily criticised. First and foremost it has *“the unpleasant property that biases increase as sample sizes increase, and that biases may be very substantial, even when errors in the location of observations are small”* (Burgman 2003: 27). Bias may be introduced by the shape of the habitat patch, and by interactions between shape, location errors, and the temporal and spatial distribution of sampling efforts (Burgman 2003: 27). Another problem is that uniform space use within the home range boundaries is assumed. However, animals are unlikely to use all parts of their home range with the same intensity and thus important information on differential space use is lost with the MCP method (Katajisto & Moilanen 2006: 406). Despite inherent problems with the minimum convex polygon method it is still widely used (Börger 2006: 1394).

### **2.2.2 Kernel density estimation:**

The kernel density estimation was introduced as a home range estimator by Worton (1989). It provides a probabilistic measure of animal space use and has the quality of directly producing a density estimate (Horne & Garton 2006b: 641). The density at any location is an

estimate of the amount of time an animal spent there. Currently, kernel methods are the standard to estimate home ranges. The problem is that a large variety of smoothing factors, kernels and sample sizes leads to a bewildering number of possible combinations for the kernel method (Gitzen et al. 2006: 1342). A series of studies investigated the influence of several aspects such as sampling strategy (Börger et al. 2006, Girard et al. 2002), observation bias (Horne et al. 2007), location error (Moser & Garton 2007), spatial and temporal autocorrelation (Katajisto & Moilanen 2006) and choice of smoothing parameter (Horne & Garton 2006b, Gitzen et al. 2006) on kernel density estimation results. The functionality of the kernel density method is explained briefly in the paragraph below. For a more detailed description refer to Silverman 1986, Worton 1995, Seaman & Powell 1996 and a recent review by Kernohan et al. 2001.

The kernel method can be intuitively described as placing a “bump”, (the three-dimensional kernel function) over each observation point in the sample. The different kernels are aggregated to form one continuous density surface. The value of the probability density at any point is estimated by summing the contribution from each kernel at that point (Horne & Garton 2006b: 641, Seaman & Powell 1996: 2076).

The kernel density estimator (for bivariate data) is mathematically defined as:

$$\hat{f}_h(x) = \frac{1}{Nh} \sum_{i=1}^N K\left(\frac{x - x_i}{h}\right)$$

Fig. 5 Mathematical definition of kernel density estimator (Seaman & Powell 1996: 2076)

where  $N$  is the number of data points,  $h$  is the smoothing parameter,  $K$  is a kernel density such as the one in figure 6,  $x$  is a vector of  $x, y$  coordinates describing the location where the function is being evaluated and  $x_i$  is a series of vectors whose coordinates describe the location of each observation (Seaman & Powell 1996: 2076).

$$K(x) = \frac{1}{\sqrt{2\pi}} e^{-\frac{1}{2}x^2}.$$

Fig. 6 Example of a kernel density

A probability surface is generated by smoothing the original observations with a smoothing parameter ( $h$ , also referred to as “bandwidth”) that has to be selected. Narrow kernel bandwidths allow close observations to have the greatest influence on the density estimate; wide kernel bandwidths allow more influence of distant observations. Narrow kernels thus reveal the small-scale details of the data, and wide kernels show the general shape of the distribution (Seaman & Powell 1996: 2077). At very small bandwidths, the density surface breaks down into single kernels (illustrated in fig. 7). Selection of large bandwidths smoothes out peaks and pits of the density surface and basically returns a flat surface (see fig. 8).

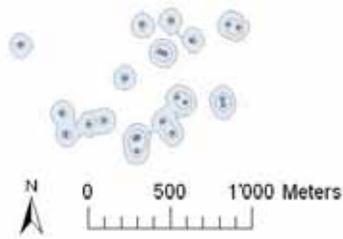


Fig. 7 Small smoothing parameter ( $h = 0.01$ ) lets the density surface break into small kernels ( $n = 22$ )

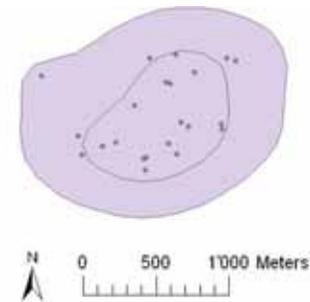


Fig. 8 Large smoothing parameter ( $h = 0.8$ ) with volume contours = 50% and 90%,  $n=22$ .

Thus, a trade-off exists for selecting the smoothing parameter. When too small, this leads to discontinuous “islands” of the utilization distribution and to smaller estimates of home range size. On the contrary, if the smoothing parameter is too large, it produces an oversmoothed estimated utilization distribution that blurs details of differential home range use which in turn leads to overestimates of home range size (Kernohan et al. 2001 in Gitzen et al. 2006: 1334).

Because kernel density estimations are sensitive to the different values of the smoothing parameter, various techniques exist to objectively select parameters (Silverman 1986 in Moser 2007: 2422). In turn, home range size estimates are thus also dependent on the methods used to calculate the smoothing parameter  $h$ . Authors have expressed their concern on the possibility that variation in  $h$  may introduce systematic variation in home range estimates that may also complicate comparisons between and even within studies (Hemson et al. 2005: 456).

The method that is most widely used is the least squares cross validation (LSCV). LSCV has become the most popular and recommended method for choosing  $h$  in home-range analysis (Kernohan et al. 2001). It is based on minimizing the integrated square error between the estimated distribution  $f'$  and the true distribution  $f$  (Horne & Garton 2006b: 642). During the process various bandwidths are examined and the one that gives the minimum for the estimated error is selected. LSCV has been found to have several disadvantages such as a high variability and a tendency to undersmooth data. Furthermore, Hemson et al. (2005: 458) showed that LSCV algorithm failed to compute at sample sizes of 300 and computation failed in 99% of attempted cases at 550 points. Gitzen et al. (2006: 1339) mainly confirm

these findings and conclude that failure rate of the LSCV algorithm increased with increasing sample size.

Another method, called “h-reference method” has been found to perform poorly except for unimodal distributions. It was therefore not recommended for general use (Seaman et al. 1999 in Kernohan et al. 2001: 144). An alternative to LSCV and reference method offered by the HRT Extension (Carr et al. 2007) is the Biased-Cross Validation (BCV). It is seen as a novel technique that could achieve a balance between the tendency of the h-reference method to oversmooth and LSCV method to undersmooth utilization distributions. BCV calculates a value of  $h$  that minimizes the estimated asymptotic mean integrated square error (AMISE) (Carr et al. 1998). However difficult the choice between smoothing parameter selection methods might be, Seaman and Powell (1996: 645-647) concluded that the fit of estimated distributions using kernels was usually more sensitive to sample size than choice of smoothing parameter.

When applying KDE methods a fundamental choice between fixed and adaptive kernels has to be made (Seaman & Powell 1996: 2083). The fixed kernel uses the same bandwidth for the whole dataset, whereas in the adaptive kernel, once a bandwidth has been selected, it is possible to adjust the density estimate. The smoothing parameter then varies so that areas with a low concentration of points have higher  $h$  values and thus receive more smoothing than areas with a high concentration of points that are less smoothed. Seaman & Powell (1996: 2084) conclude that adaptive kernels give the best density estimate at the actual observation locations, whereas fixed kernels give the best overall surface estimate.

Once the utilization distribution has been estimated, the density is converted into a home range estimate. Contours that connect areas with equal density can describe usage of the area. Many studies define the home range as the area enclosing 95% of the utilization distribution (Seaman & Powell 1996: 2077, Worton 1989), but 90% contours have been judged more appropriate (Börger et al. 2006: 1393). For a conservative and reliable estimate of home ranges using the 90% volume contour for both fixed and adaptive kernels is recommended. This suggestion is supported by Börger et al. (2006: 1402) who claim that the commonly used 95% isopleth should be avoided. In contrast to the 95% volume contour they recommend isopleths between 90% and 50%.

### **2.2.3 Observation bias**

Home ranges are typically modelled from a sample of observations that is used to estimate the utilization distribution (Kernohan et al. 2001: 135). If observation bias is present in data used to estimate the utilization distribution it will bias the results (Horne et al. 2007: 996). If a location is more likely to be sampled, it will result as an area with higher probability of occurrence in the utilization distribution. The inferences drawn from this result are biased

because the area is not intensively used by the animal (e.g. due to resources). On the contrary, if an area is less intensively sampled due to technical reasons or because it is difficult to access (e.g. steep terrain, dense forest) this area will get a low probability of occurrence in the utilization distribution, even though it could be biologically important for the studied animal. In Tuanan, an observation bias might occur: if researchers are looking for animals in the forest, they walk out from camp, usually on the same boardwalks, and from there to the different parts of the study area. It was hypothesized that the possibility of encountering an animal is higher close to boardwalks.

#### **2.2.4 Temporal and spatial autocorrelation**

For almost 20 years, much attention has been paid to the effect of autocorrelation in animal location data (Kernohan et al. 2001: 128). The issue of autocorrelation has been conversely discussed in the scientific literature. Swihart and Slade (1985) see independence of observations and therefore the absence of autocorrelation as a prerequisite for meaningful home range estimations. Reynolds and Laundré (1990) and de Solla et al. (1990) on the other hand suggest that autocorrelation is characteristic for wildlife ranging data and should not be removed, because autocorrelated data contains biologically meaningful information.

Autocorrelation exists when locations at time  $t$  are dependent on the animal's location at time  $t - 1$  (Swihart and Slade 1985: 1176). This allows the prediction of an animal's location at  $t + 1$  based on the location at  $t$ . Autocorrelation in a dataset occurs if:

- the animal has too little time to move away between consecutive observations
- the animal does not move between consecutive observations
- the animal periodically returns to the same portion of its home range

It is often the case in animal space-use studies that bursts of data are collected separated by gaps where no data are obtained. Any two successive sightings in such high frequency sampling are almost certain to be in close proximity because of limitations in an animal's mobility. The accumulation of autocorrelation in such data is unavoidable (Dunn & Gipson 1977: 86). Autocorrelation poses a problem in home range studies because  $n$  autocorrelated observations are less informative than  $n$  independent observations. Home range size will therefore be underestimated with autocorrelated data.

The so called "time to independence" between successive locations is the time interval that is necessary to achieve statistical independence between two locations. This was expressed as the ratio between the mean squared distance between successive observations ( $t^2$ ) and the mean squared distance from the centre of activity ( $r^2$ ). The  $t^2/r^2$  ratio is also known as Schoener's Index (Schoener 1981). McNay et al. (1994: 422) pointed out some problems with the Schoener's ratio: time to independence will be unrealistically long if animals are migratory or sporadically visit infrequently used parts of their home range. As

Schoener's ratio test is entirely based on the distance between successive observations related to the distance from the activity centre, animals that do not move around a centre of their home range such as a den or a nest will have an unrealistically long time to independence. Following Schoener's original approach Swihart & Slade (1985) developed their own index of statistical independence of observations. A time to independence was calculated by successive subsampling until independence according to Schoener's  $t^2/r^2$  ratio was achieved at three successive sample intervals. This index has since been used by many authors to assess the degree of temporal autocorrelation in location data (Rooney et al. 1998: 80).

Recent evidence however suggests that the problem of autocorrelation for home range studies has long been overestimated. Gese et al. (1990: 501) pointed out that there was no difference in home range estimates based on independent versus sequential locations. Even the opposite was shown by Reynolds & Laundré (1990: 319): for coyotes (*Canis latrans*) and pronghorns (*Antilocapra americana*) home range size was underestimated when using observations with intervals that were considered independent. The question addressed was whether autocorrelation has a significant effect on home range size estimates. A comparison of home range estimates from two different datasets with different amounts of autocorrelation would be likely to show the effect of autocorrelation, if present. It was hypothesised that autocorrelation has no significant effect on orangutan home range size estimates with kernel density methods.

### **2.2.5 Selecting a home range model**

Researchers strive to find objective criteria for evaluating the performance of different home range models (Horne & Garton 2006: 1146). Models have been reviewed using several techniques such as comparing methodology and assumptions of different models and by computer simulations (White and Garrot 1990: 175). For example, Kernohan et al. (2001: 133) evaluated 12 different home range models based on various criteria such as required sample size, robustness to autocorrelated data and sensitivity to outliers. In their evaluation fixed and adaptive kernel method performed better relative to the minimum convex polygon. However, Horne & Garton (2006: 1147) criticise model selection based solely on methodical considerations or simulated data. Despite the power to use simulations to evaluate models, those studies often show that the performance depends on the assumed "true" distribution of the simulated data. Although the properties of the simulated data drawn from known distributions are well understood, these properties may not mimic the irregularities exhibited by real data sets closely enough (Hemson et al. 2005: 461). As a solution to model selection, Horne & Garton (2006: 1147-1151) propose to apply the information-theoretic approach to model selection. This approach helps to decide which

model of a set of approximating models is closer to truth than other. It is based on the assumption that all models are only estimates of reality and that no model is ever “true” or performs well in all situations. The question to be answered then is: which model of a set of models has the best support from the data? Based on the information theoretic model selection, the “best” model can be defined as the one which has the smallest deviation between the approximating and the “true” model. This provides an objective measure for the adequacy of a home range model for a given data set. The Kullback-Leibler (KL) distance is used as an indicator of this discrepancy and is formally defined as the “information lost” when a fitted model ( $f(x)$ ) is used to approximate the true model ( $f(f(x))$ ). The mathematic definition of the Kullback Leibler distance is:

$$KL(f, \hat{f}) = \int f(x) \ln \left( \frac{f(x)}{\hat{f}(x)} \right) dx$$

Fig. 9 Kullback-Leibler distance (Horne & Garton 2006)

where  $f$  is the true probability density of random variable(s)  $x$  and  $f'$  is the probability density of the approximating model (Horne & Garton 2006: 1147).

Because the true underlying distribution is unknown, the KL distance can not be calculated directly. Various criteria have been developed to estimate the KL distance. The one that will be used in this study is the likelihood-cross validation criterion (CVC), because it is also able to compare nonparametric models such as the fixed and adaptive kernel methods. The CVC is defined as

$$CVC = -2 \times \sum_{i=1}^n \ln \hat{f}_{-i}(x_i)$$

Fig. 10: Likelihood cross-validation criterion for  $i = 1$  to  $n$  samples (Horne & Garton 2006)

where  $f_{-i}(x_i)$  is the density calculated for sample  $x_i$  without that sample being used to estimate  $f'$  (Horne & Garton 2006: 1147) .

## 2.3 Methods

### 2.3.1 From forest to files – methods of field data collection and processing

In Tuanan and other field stations for orangutan research, data are collected using a standardized field protocol. Every 2 minutes the behaviour of the focal animal is noted using the standard protocol (see <http://www.aim.uzh.ch/orangutanetwork/FieldGuidelines.html>, accessed 3.4.2008). In addition to the behavioural data a map of the animal's path is drawn (figure 11).

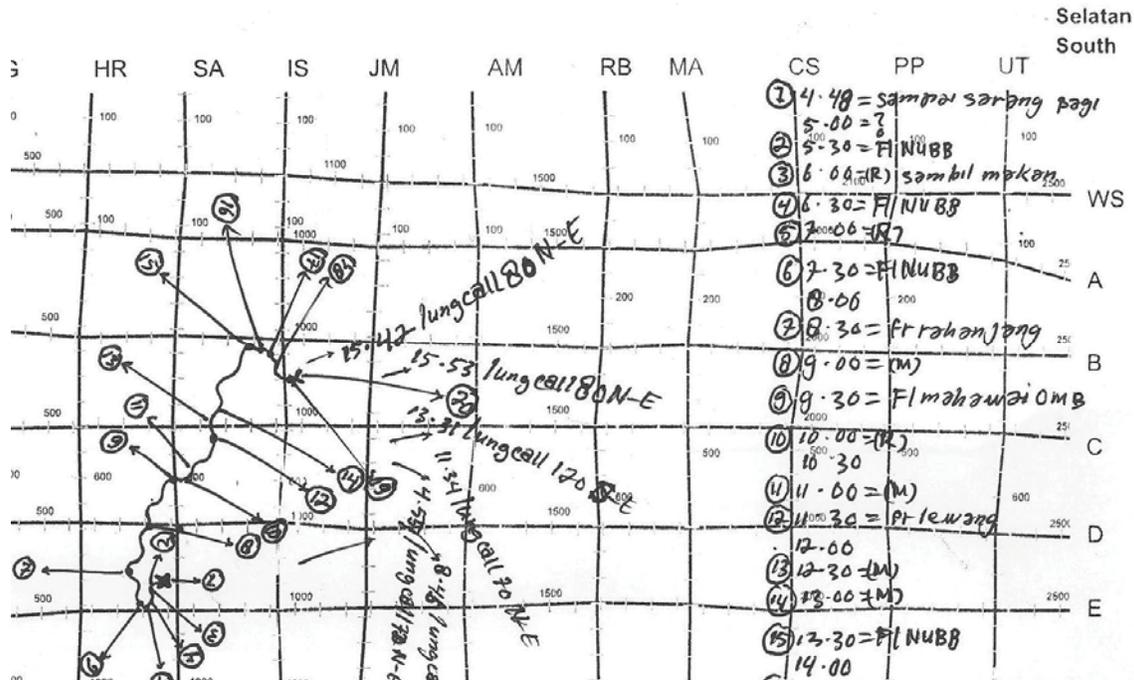


Fig.11: Detail of a focal map (16.7.2008, Kerry and Kino)

Usually two people follow a focal animal: one person is taking behavioural data while the other one is drawing the map. If an animal is found in the study area, it is followed at a distance of at least 10 meters until it builds its night nest. The next morning the orangutan is followed from its nest until its next night nest. This procedure is continued for a maximum of ten days (to minimize stress for the animals) or until the animal is lost or leaves the study area. In the map of the research area, transects and boardwalks are mapped and 50m marks are indicated. In the forest, every 50m a tag has been placed on a tree that enables the identification of the transect name and verification of the current position on the map. Followers are equipped with a compass that allows them to estimate the direction of the focal animal. For every individual, every half hour the location is noted as well as the morning and night nest and food trees used for longer than 10 minutes. All follow data are sent to the University of Zurich, where they are processed and stored. Behavioural data are entered into an access-database (Microsoft); maps are digitized in ArcGIS version 9.1 (ESRI 2005) by

manually adding points on a reference grid (the digitalized and georeferenced map) in the same position as in the field map. Additional data (name of focal animal, time, date, nest location, species of fruit eaten etc.) are entered in an attribute table. Currently, data on orangutan positions is being collected manually, whereas data to produce a cartographic map was collected with GPS.

In order to check the quality of follow maps a hand-held GPS device was taken to the field. The device used was GPSMAP<sup>®</sup> 76CSx (Garmin Ltd., Southampton SO40 9RB, UK). Locations were mapped by observers while GPS position of the focal animal was recorded at the same time. GPS data were recorded as geographic coordinates (latitude/longitude) with the reference ellipsoid WGS 1984. They were transformed into Universal Transverse Mercator (UTM) coordinates into the WGS 1984 UTM Zone 50S using the CoordTrans program v2.30 (Franson Technology, Sweden). Map data were manually digitized in ArcGIS v. 9.2, (ESRI). Three different follow days were analysed. In these examples, inter-observer variability can be excluded, because all the maps were drawn by the same person. GPS and map points were connected and the length of the line calculated. For vector-based line features such as daily paths represented in orangutan follow maps the most popular location error model is the epsilon band. It is a band of usually 2 standard-deviations around the digitized line serving as a buffer of uncertainty (Leung & Yan 1998: 607). A 10m and 25m buffer was created around the GPS line as a location-error band (epsilon-band) to visually assess differences in both lines. The 25m buffer around the GPS line was intersected with the manually mapped line to quantitatively determine the distance of the line that lay inside and outside the buffer. GPS precision was measured by recording the GPS inaccuracy measurement provided by the GPS device. A total of 665 samples were collected, either in the forest during follows, mapping and searching or on camp days with exact date and time. An estimate of weather situation (clouded or sunny, rain or no rain) was also included. For GPS data it was tested whether the signal accuracy differs significantly between the two locations “forest” and “camp”. The two locations were contrasted with a comparison of means. To qualitatively check whether the anecdotal evidence for bad position acquisition during the afternoon was an effect of satellite geometry, the Trimble Planning<sup>®</sup> program v. 2.7 (Trimble Ltd, CA 04985, USA) was used. It allows visualizing satellite availability for a specific geographical location on a specific date.

### **2.3.2 Model selection**

Calculation of information criterion for information-theoretic based model selection was done using the program “HomeRangeSelect” written in Visual Basic (Supplement 2 in Horne & Garton 2006). Likelihood cross-validation (CVh) is implemented in the software as the

method to choose the smoothing parameter for kernel estimates. Random selections of orangutan location data of four females (Juni, Jinak, Kerry and Mindy) were evaluated. Samples were drawn from the total distribution data orangutan females for the years 2005/2006. Sample sizes greater than 100 could not be evaluated due to computational limitations of the program.

### **2.3.3 Comparison of home range models**

The home range models *fixed* and *adaptive kernels* as well as the *minimum convex polygon* method were compared, using data from the same four females. Six different sample sizes (25, 50, 100, 500, 1000 and 2000) were analysed for the different models. A random subsample from all locations obtained for each individual for the period of 2003 until Mai 2007 was selected using Hawth's Analysis Tools (Beyer 2004), an extension to ArcGIS v. 9.2 (ESRI). MCP was calculated using the method implemented in Hawth's Tools (Beyer 2004), with 95% of all points selected by a "floating mean" algorithm. This method calculates the arithmetic centre of all points, and then drops the farthest single point. The mean is recalculated from the subset of points and the next point is dropped. This procedure is continued until the 95% of points remain selected (Rodgers & Carr 1998). In order to solely test the effect of sampling size (without sampling size influencing smoothing parameter selection)  $h$  was held constant at some arbitrarily defined value of 0.3. In this study, volume contours were calculated in 10% steps from 10% to 90%, but only 90% and 50% volume contours are reported.

The effects of parameter selection by Least-Squares Cross-Validation, Biased Cross-Validation and the reference method ( $h_{ref}$ ) were explored for different data sets. Smoothing parameter selection was done with the aforementioned methods implemented in HRT (Home Range Tools for ArcGIS®, version 1.1 by Rodgers et al. 2007). A user-defined bandwidth of 0.3 and 0.7 for fixed kernel, and 0.3 for adaptive kernel were also included in a preliminary analysis. The user-defined bandwidths were defined by visual inspection of the results in order to generate "visually attractive" home-ranges, e.g. a continuous surface with no holes.

Based on these analyses, means between groups were compared using ANOVA, Kruskal-Wallis or Man-Whitney-U test, depending on the distribution of data (SPSS v. 14.0 for Windows, by SPSS Inc., Chicago IL 60606, USA) to determine significant effects on home range size estimates.

### **2.3.4 Observation bias and autocorrelation**

To detect if an observation bias was present in the data, all locations of a newly found animal were selected. These points were intersected with a 100m buffer around the boardwalks in the study area (WS, AI, KS, JM and CK, see Annex 1). To test for the amount

of autocorrelation present in the spatio-temporal orangutan data of Tuanan, Schoener's index and Swihart & Slade's index (Swihart & Slade 1985) were evaluated as measurements of autocorrelation for the four females with different sample sizes. In an attempt to reduce autocorrelation in one dataset, a sampling strategy was employed that would reduce autocorrelation in the data but that did not use "destructive subsampling" (de Solla 1999: 221). Rather, a subsampling scheme that reduced the number of observations based on biologically meaningful criteria was needed. Therefore, only orangutan night nests' locations that are separated by a time gap of approximately 24 hours were used rather than the half-hour observations from follows. As total number of recorded night nests varies between females, nest locations were randomly subsampled at  $n = 100, 50$  and  $25$  to obtain equal sample sizes for all females. Morning nest locations were excluded from the analysis to avoid recording the same locations twice for the same nests (the nest location is recorded both in the evening when the orangutan builds its nest and the following morning). Home range sizes were tested for significant differences in means with a with a paired-t test in SPSS v. 14.0 (SPSS Inc. Chicago, IL 60606, USA).

## 2.4 Results

### 2.4.1 GPS location error

The mean GPS reported location error in Tuanan was 9.79 metres ( $\pm 3.432$ ,  $n = 665$ ). Of the measured locations, half lay within 9 metres of the “true” location and 95% had a location error of less than 18 metres. Mean location error was higher in camp ( $11.3 \text{ m} \pm 4.2$ ,  $n = 237$ ) than in the forest ( $9.0 \text{ m} \pm 2.6$ ,  $n = 428$ ). Differences between locations (forest and camp) were significant (ANOVA,  $F = 79.411$ ,  $p < 0.05$ ). The effect of cloud cover was contradictory. On days with cloud cover, mean location error was lower ( $9.23\text{m} \pm 2.90$ ,  $n = 349$ ) than on days with sporadic cloud cover ( $10.41\text{m} \pm 3.85$ ,  $n = 316$ ). Differences in location error between days with and without cloud cover were also significant (ANOVA,  $F = 20.150$ ,  $p < 0.05$ ). Mean location error was  $9.88\text{m} (\pm 3.44, n = 514)$  on days with no rain and  $9.51\text{m} (\pm 3.4, n = 151)$  on rainy days. Differences in means were not significant (ANOVA,  $F = 1.325$ ,  $p > 0.05$ ). Rain thus did not negatively affect the GPS signal.

Satellite availability was checked with the Trimble Planning program for different times of the day. During the afternoon from 1 PM to 2 PM sometimes only 4 satellites were available (fig. 12), the absolute minimum for a three-dimensional fix.

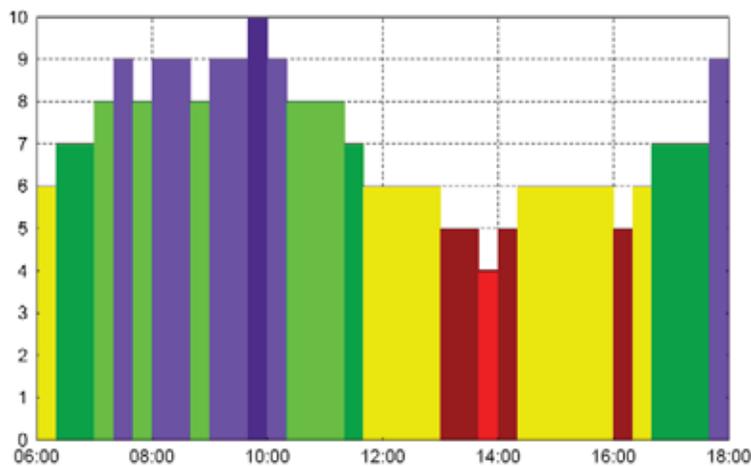


Fig. 12 Number of available satellites at different times of the day (22.1.2008) for the Tuanan station

If some of the 4 satellites at this time also have a low elevation, obtaining a location fix can become difficult. Only one or two satellites at low elevations would have to be obstructed by trees to make localisation impossible.

Exactly this is the case for Tuanan (fig. 13). At 2 PM the highest available satellites are at an approximate elevation of  $63^\circ$  and  $42^\circ$  respectively, while the others are all below  $30^\circ$ . The problem of acquiring position fixes in the afternoon can thus be explained by satellite geometry.

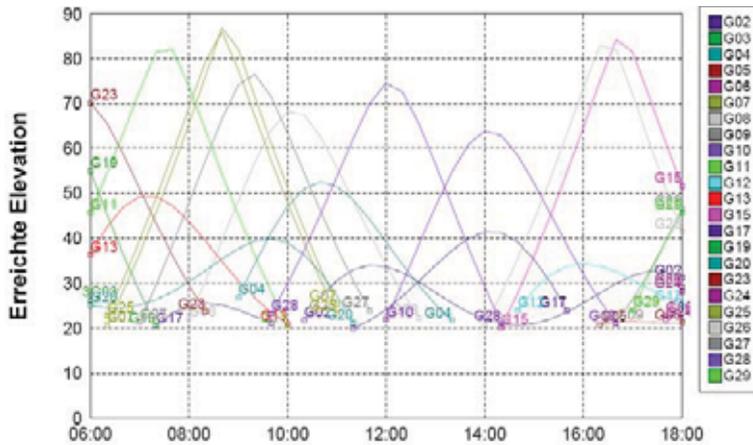


Fig. 13 Elevation (> 20°) of satellites at different times of the day at 22.1.2008 for Tuanan station

To take all factors into account and evaluate their importance, a univariate analysis of variance was performed on the ln-transformed values of the GPS location error. The overall model was significant (ANOVA,  $F = 13.301$ ,  $p < 0.05$ ) and was able to explain more than 40% of variance in location error (R Squared = 0.433, Adjusted R Squared = 0.400). Canopy cover was significant in the model ( $F = 104.324$ ,  $p < 0.05$ ) as was cloud cover ( $F = 9.765$ ,  $p < 0.05$ ) and time of the day ( $F = 8.761$ ,  $p < 0.05$ ). The effect of rain was not significant ( $F = 0.991$ ,  $p > 0.05$ ). Of all factors, canopy cover and time of the day had the highest partial  $\epsilon$ -squared values (0.142 and 0.154, respectively), indicating their relative importance in explaining variance in location error.

#### 2.4.2 Comparison of field methods

For Jinak and her infant Jerry (see fig. 14) the daily travelled distance on 26<sup>th</sup> January 2008 was estimated with GPS-based points to be 872 meters. With the map it was estimated to be 845 meters, underestimating path length by 3%. Intersecting the map line with a 25m buffer of the GPS line showed that 204 meters or 25% of the map line lay outside the buffer. Thus 75% of the map line was within 25 meters of the GPS line.

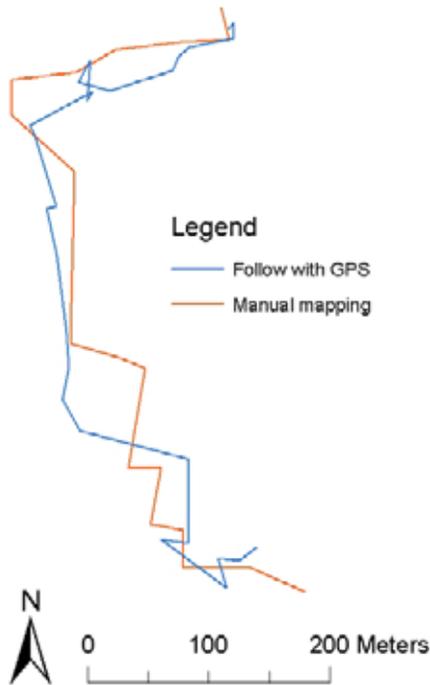


Fig. 14 Comparison of manual mapping and GPS line of Jinak (26.1.2008)

Note that in figure 14 the line drawn from GPS points has several small-scale self-intersections, a feature that is difficult to represent with paper and pencil at the scale of the paper map. Follow data of Jinak for 9<sup>th</sup> February 2008 yielded similar results. Travelled distance calculated from map line was estimated at 932m, while the GPS line length was 927m. The difference between the two lengths was less than one percent of the map line (5m or 0.5%).

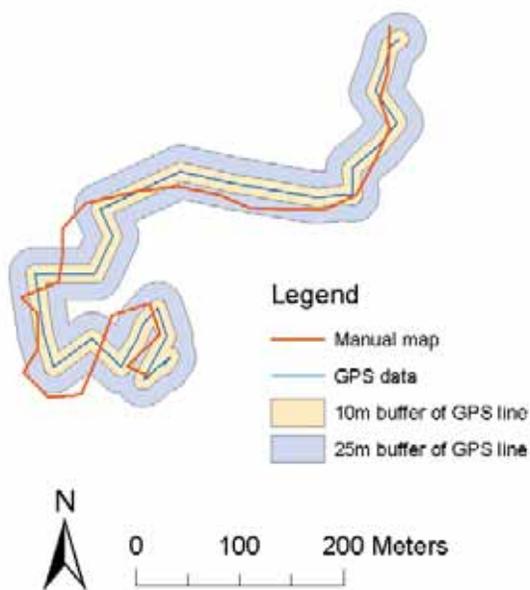


Fig. 15 Comparison of map and GPS lines for Jinak on 9.2.2008 with 10 and 25m buffers

Map line intersected with the 25m buffer showed 86% of the map line lay within the buffer (see figure 15). Another mother-infant dyad that was followed in the study period was Desy and her infant Dery. The length calculated from GPS on the follow of 17. February 2008 was 489 meters, whereas the map line was 414 meters long. The map line was thus 84% of the GPS line length. More than 75% or 315 meters lay inside the 25 m buffer of the GPS line. Note that in this example path lengths are shorter for Desy than for Jinak because Desy was encountered in the forest after 1PM and not a whole day-path was recorded. The three examples show that between 75% - 86% of mapped lines were within a 25m error-band of the GPS line. Approximately 80% of travel paths lay less than 25 meters apart from the “true” location, indicating high accuracy of manual maps compared to the “true” lines measured with GPS points.

### 2.4.3 Model selection

Kernel density estimators almost always outperformed other home range estimators (bivariate normal distribution with one or two centres).  $\Delta\text{CVC}$  values indicate the relative support for a certain model. Table 1 shows the results obtained for a comparison of different home range models and sample sizes for one female. Low  $\Delta\text{CVC}$  values indicate low deviation between the examined model and the “best model”.

Sample size	1 Mode Bivariate Normal	Fixed Kernel	Adaptive Kernel
20	3.5	<b>0</b>	2.1
30	4.1	0.1	<b>0</b>
50	7.6	<b>0</b>	2.4
90	34.1	<b>0</b>	8.1

Tab. 1:  $\Delta\text{CVC}$  between best and selected model with data from Jinak

Except in one case, fixed kernel was always selected as the best approximating model with the lowest CVC value. Even when the fixed kernel did not have the lowest  $\Delta\text{CVC}$  value, it was included as a competing best model (as defined by Horne & Garton 2006 when  $\Delta\text{CVC}$  is  $< 3$  between two competing models). At small sample sizes, adaptive kernel was twice included as a best competing model. In order to test the assumption drawn from comparison for the dataset of Jinak, 3 other females (Juni, Kerry and Mindy), all of them with infants, were included in the analysis as well. Bivariate normal distribution shows high  $\Delta\text{CVC}$  for all sample sizes and females.

Sample size	1 Mode Bivariate Normal	Fixed Kernel	Adaptive Kernel
20	9.9	<b>0</b>	1.3
30	10.4	<b>0</b>	5.9
50	9.2	<b>0</b>	18.5
90	31.7	<b>0</b>	13.2

Tab. 2:  $\Delta\text{CVC}$  between best and selected model with data from Mindy

For the females Kerry and Juni, adaptive and fixed kernel were equally chosen, but for Mindy, fixed kernel outperformed adaptive kernel for all sample sizes and clearly suggest fixed kernel as the best competing model (see tab. 2).

#### 2.4.4 Minimum convex polygon method and its sensitivity to sample size

With minimum convex polygon method, home range size estimates increased with increasing sample size for the four females (see tab. 3 and fig. 14).

Model	Sample size	Mean	N	Std. Deviation
MCP	25	138.22	4	69.08
	50	166.13	4	55.30
	100	223.23	4	89.78
	500	251.69	4	80.45
	1000	265.10	4	83.83
	2000	287.26	4	103.56
	Total		221.94	24

Tab. 3 Relation of sample size and home range estimates for MCP

For example for Juni, home range size increased by 70% from 25 locations to 500 locations (201 ha to 342 ha). At the largest sample size (n = 2000), home range size was estimated at almost 400 hectares, increasing by 50% as compared to the smallest sample size. Increase in home range size was almost monotonic with a small drop at the sample size 1000. Figure 17 graphically represents increase in home range size estimates with sample size.

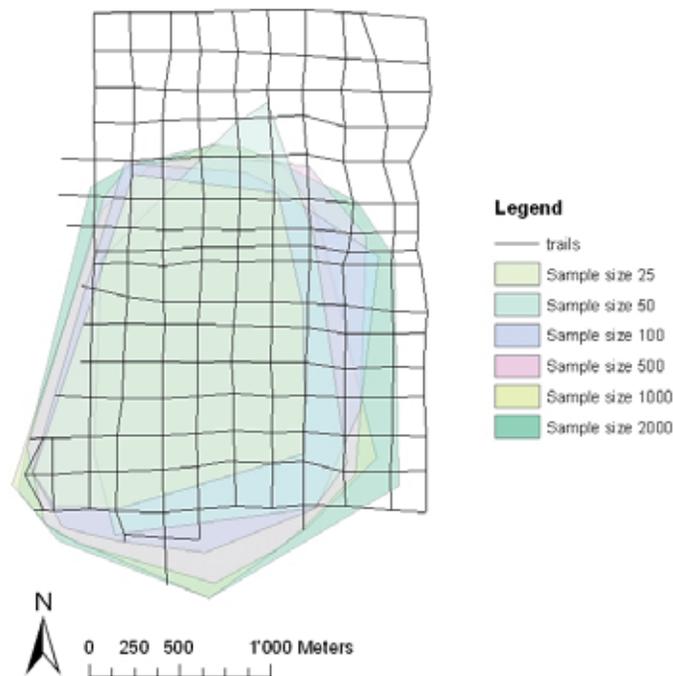


Fig. 16: Home range shapes with the MCP method for different sample sizes for Juni.

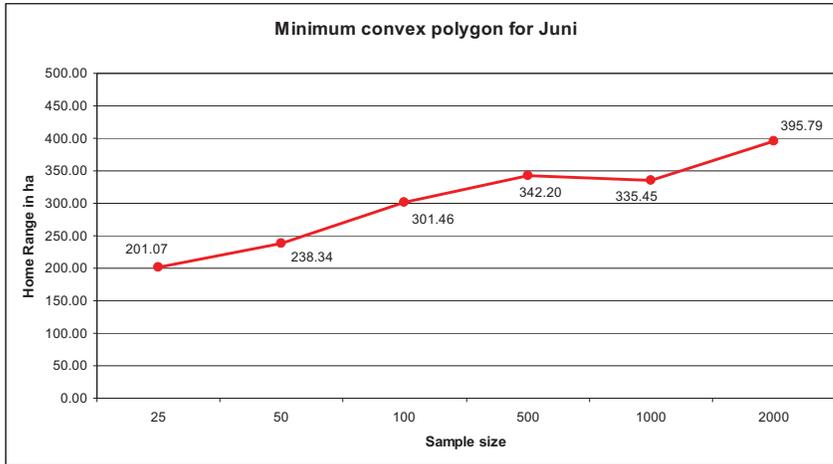


Fig. 17: No asymptote was reached at sample size = 2000.

#### 2.4.5 Kernel estimation - fixed or adaptive?

A comparison of fixed and adaptive kernel showed that adaptive kernels oversmoothed location data. In figure 18 it can be seen that the outermost isopleth (95% volume contour) includes an additional area of 82 hectares based on relatively few points. The increase in area from the 90% to the 95% volume contour based on such few locations is 43%. With the same distribution and same smoothing parameter but fixed kernel, the increase in home range size from 90% to 95% is only 28% or 51 hectares. Adaptive kernel oversmoothed the location data, especially towards the outer parts of the home range. The 95% volume contour for fixed kernel also included areas based on as little as two points (see south-western part of the home range for fixed kernel). Therefore, the 90% volume contour gave a more conservative area estimation that had more support from location data and results were reported based on 90% volume contours.

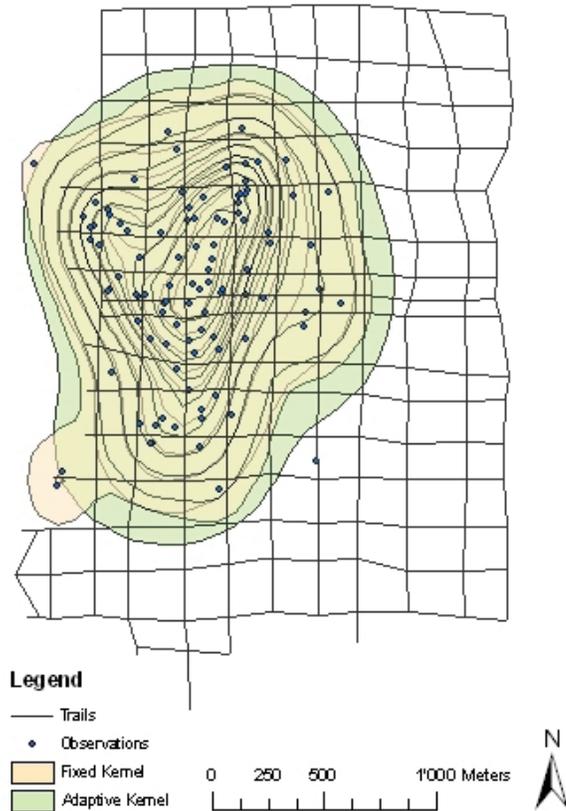


Fig. 18 Adaptive kernel versus fixed kernel density estimation for the female Mindy ( $n=100$ ,  $h = 0.45$  estimated with BCV with volume contours from 95, 90, 80, 70%...10%)

#### 2.4.6 Influence of smoothing parameter

For all females  $h$  was always smaller when estimated with BCV than with the reference method. When compared with LSCV, BCV usually produced less variable results that lay between  $h_{ref}$  and  $h$  estimated with LSCV, indicating the balance BCV strikes between under- and oversmoothing. LSCV method failed to compute at large sample sizes. It can be observed in table 4 how the selected  $h$  shows values  $< 0.1$  at sample sizes  $> 100$ . In contrast to LSCV, BCV never failed at large sample sized and produced sensible results for all sample sizes.

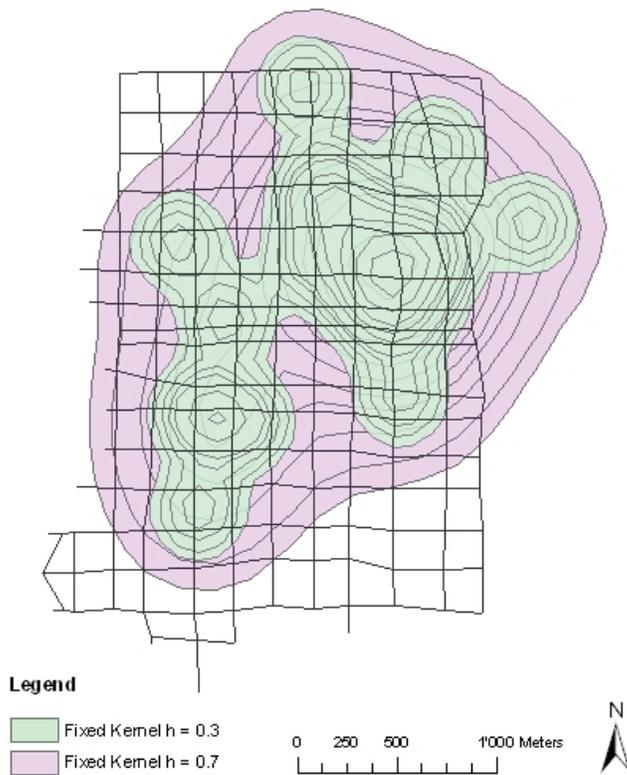


Fig. 19 Comparison of small and large bandwidths for fixed kernel home range estimations

Sample size	BCV	$h_{ref}$	LSCV
25	0.5701	0.5848	0.3544
50	0.4314	0.5210	0.3972
100	0.4525	0.4642	0.3655
500	0.3461	0.3550	0.1198
1000	0.3082	0.3162	0.0584
2000	0.2746	0.2817	0.0292

Tab. 4 Smoothing parameters estimated with different methods for various sample sizes (Mindy)

#### 2.4.7 Finding the sample size for kernel home range estimates

With a constant smoothing parameter of  $h = 0.3$  and fixed kernel, home range sizes steadily increased with increasing sample size to a certain point where they seem to reach an asymptote. For example for the female Juni, increase was steep at small sample sizes, with more than 10% increase in home range size for steps between sample sizes 25, 50 and 100. At  $n = 500$  range estimates reached and asymptote as increase remained below 2% or was even slightly negative (-1.25% from  $n = 500$  to  $n = 1000$ ). Total increase in estimated home range size with constant smoothing parameter from lowest sample size to largest for Juni was 42% or 124 hectares (figure 20).

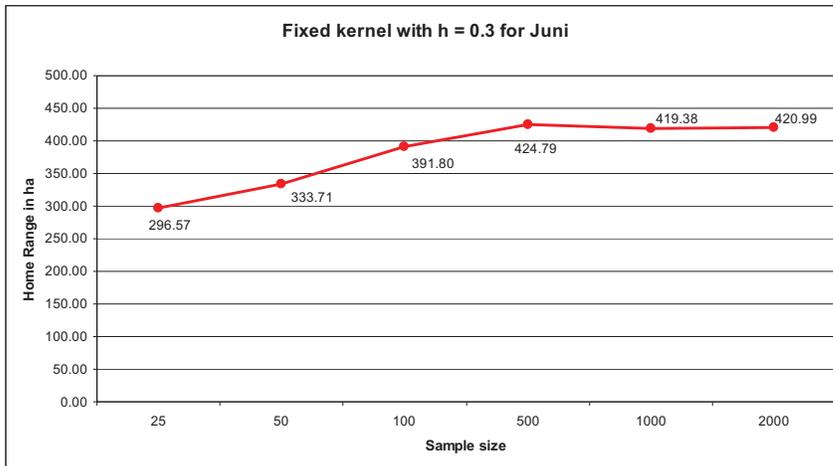


Fig. 20 Fixed kernel density estimation with smoothing parameter  $h = 0.3$  for Juni.

Increase in home range size estimates with constant smoothing parameter for increasing sample sizes is illustrated with the Ln-transformed values in figure 21.

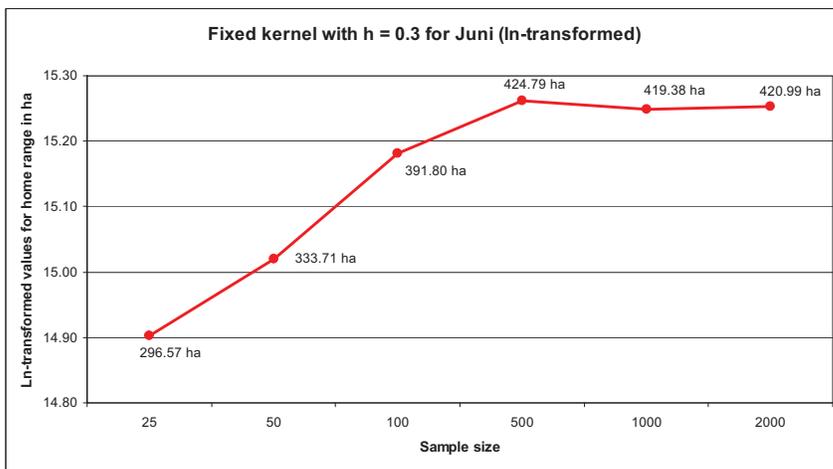


Fig. 21 Ln-transformed scale for home range size of female Juni

However, as holding the smoothing parameter constant will undersmooth locations at low sample sizes and oversmooth at high sample sizes, the objective method of biased-cross validation was used. Under these conditions, home range size decreased with increasing sample size. For all females, the table 5 indicates the same pattern. Ranges increased up to  $n = 100$  and then started to decrease again. The local “peak” of home range size at  $n = 100$  is not caused by a peak in  $h$ . Rather, smoothing parameters decreased monotonically for most females. Smoothing parameters thus had no direct relation with home range size estimates. Range estimates are almost identical for the smallest and largest sample size (301 and 303 ha, respectively). Although range estimates are similar for all females at smallest and largest sample size, variation of home range shapes and sizes due to random subsampling was large at low sample sizes (see figure 24).

Model	Sample size	Mean	N	Std. Deviation
Fixed Kernel	25	301.60	4	122.47
	50	331.74	4	119.18
	100	374.94	4	116.61
	500	328.84	4	113.60
	1000	315.95	4	104.55
	2000	303.02	4	106.96
	Total	326.02	24	104.02

Tab. 5 Relation of sample size to range estimates with fixed kernel

For example for Juni, largest home range size was estimated with sample size  $n = 25$  (473 ha) and smallest with  $n = 2000$  (408 ha). The decrease is clearly visible in figures 22 and 23.

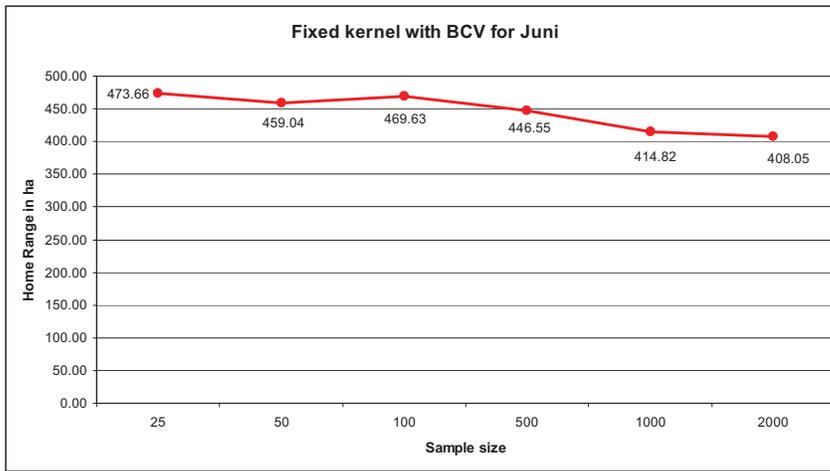


Fig. 22 Fixed Kernel home range size estimates for Juni

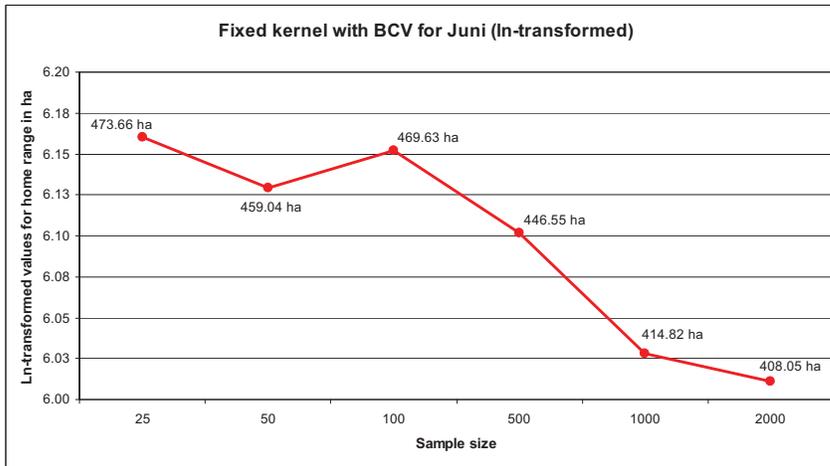


Fig. 23 Log-transformed values of home range size indicating the decrease in home range size estimates with increasing sample size for Juni

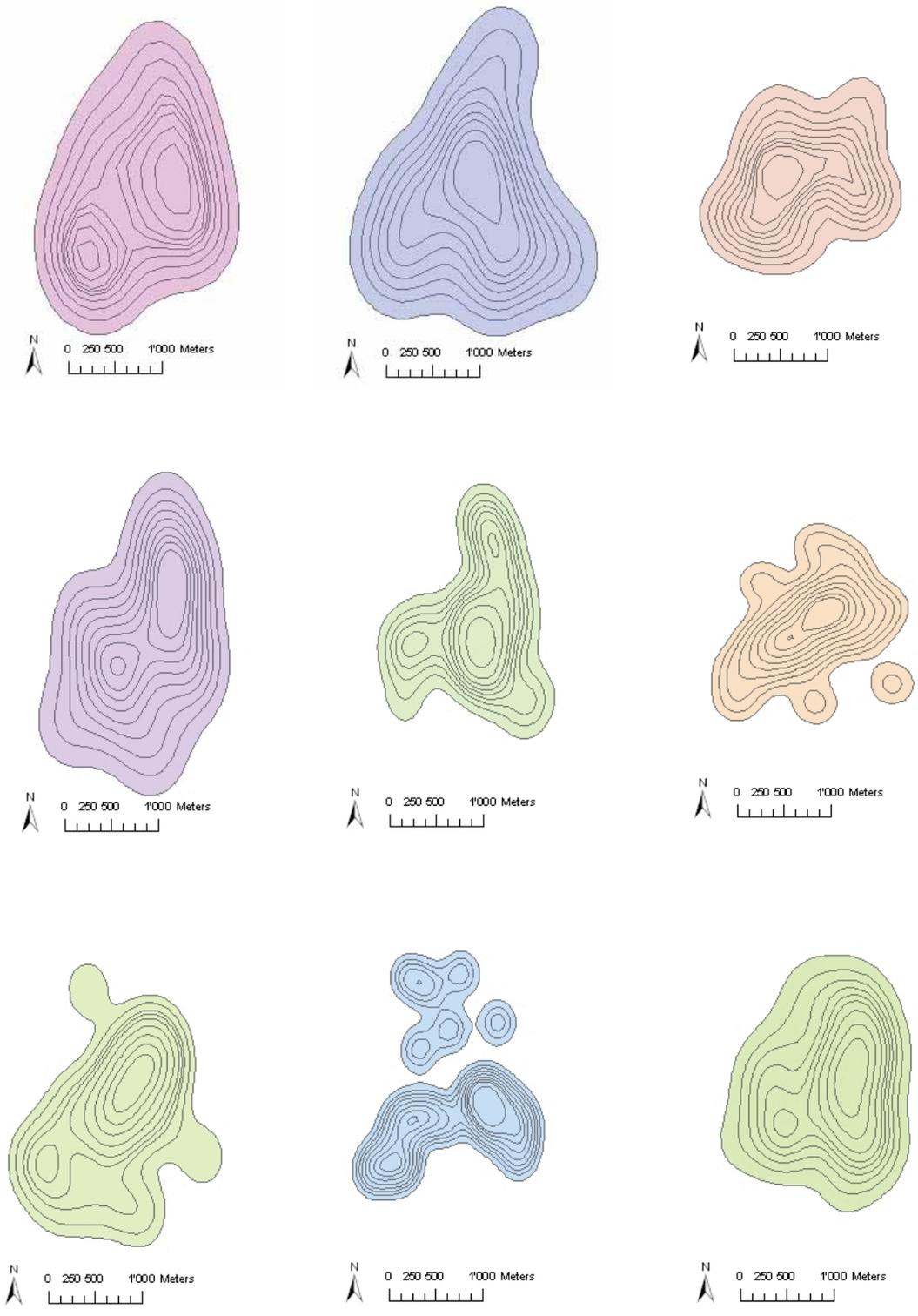


Fig. 24 Variation in home range size and shapes is large, especially at small sample sizes (individual Juni, n = 25, fixed kernel, 90% - 10% volume contour, h estimated with BCV)

A graphic depiction of home ranges across sample sizes shows that home range shapes stabilize at high sample sizes, although they decrease in size (see figure 25).

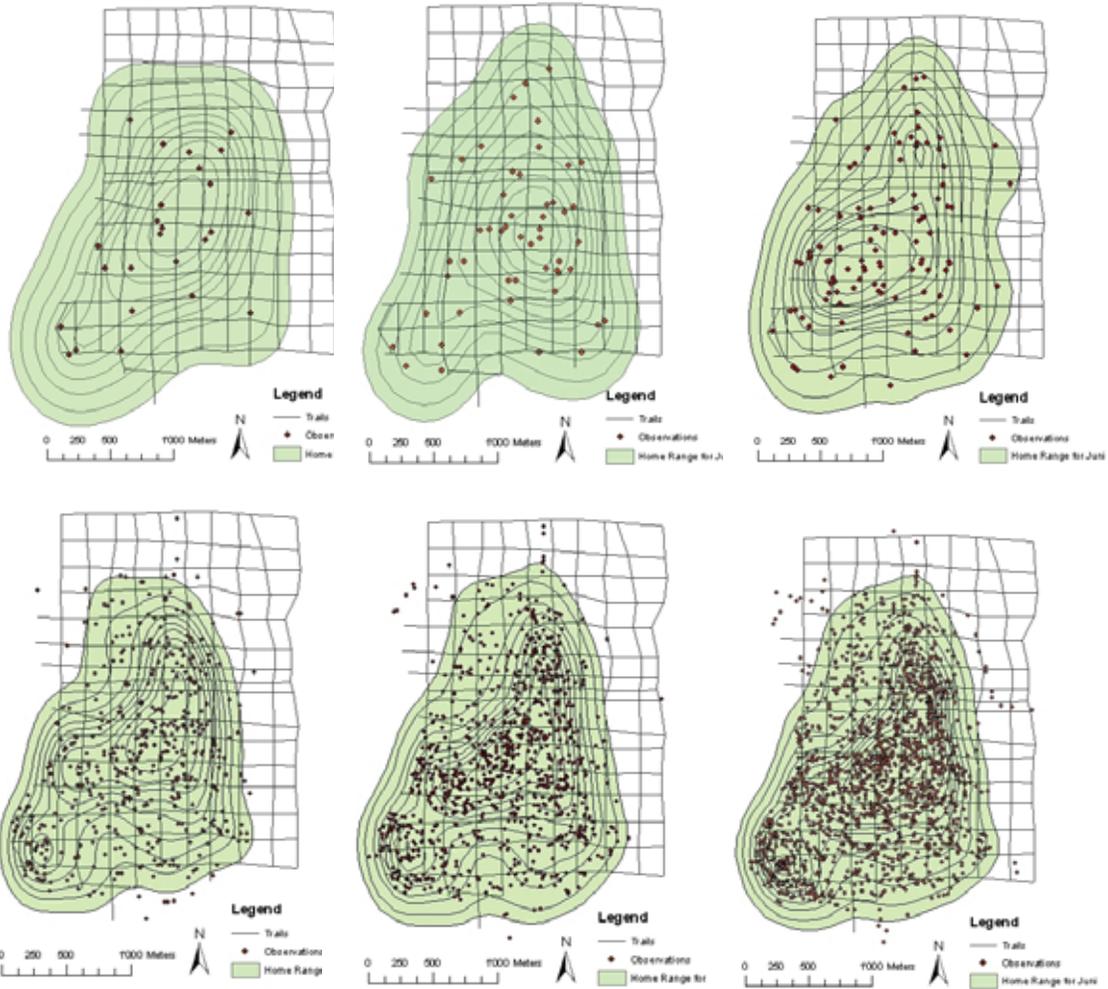


Fig. 25 Change in home range size and shape for different sample sizes (individual Junco,  $n = 25, 50, 100, 500, 1000$  and  $2000$ ,  $h$  estimated with BCV, 95% - 10% volume contour)

#### 2.4.8 Influence of models, sample sizes or individuals on home range estimates

Differences in home range sizes between individuals were significant, across models and sample sizes (Kruskal-Wallis, Chi-Square 40.744,  $p < 0.05$ ).

Individual	Mean	N	Std. Deviation
Jinak	253.28	18	71.85
Juni	418.48	18	102.21
Kerry	375.36	18	100.91
Mindy	187.22	18	48.90
Total	308.58	72	124.30

Tab. 6 Differences between individuals in range size estimates (Note:  $n = 3$  methods at 6 sample sizes)

Differences between sample sizes were not significant across models and individuals (Kruskal-Wallis, Chi-Square,  $p > 0.05$ ), and sample size did not correlate with home range

size estimates (Spearman's  $\rho = 0.098$ ,  $p > 0.05$ ). Differences between home range models were significant (Kruskal-Wallis, Chi-Square = 19.766,  $p < 0.05$ ). The adaptive kernel produced largest range estimates ( $377.8 \text{ ha} \pm 124.5$ ,  $n = 24$ ), fixed kernel intermediate ( $326.01 \pm 104.02$ ,  $n = 24$ ) and MCP smallest ( $221.94 \pm 90.6$ ,  $n = 24$ ). A univariate analysis of variance showed that the model including type of home range model, individual and sample size was able to explain 80% in variance of home range estimates (R-Squared = 0.806, Adjusted R-Squared = 0.767). Factors entered as significant were type of home range model ( $F = 47.535$ ,  $p < 0.05$ ) and individual ( $F = 42.722$ ,  $p < 0.05$ ). Those factors also had high partial- $\epsilon$  squared values (0.684 and 0.660, respectively), which indicates their relative importance in explaining variance in range size estimates. Model type and the individual study animal were thus important factors to explain home range sizes, whereas sample size was not.

#### 2.4.9 Observation bias in orangutan location data

Out of 437 locations of newly encountered focal animals, 249 (56.98%) lay within the borders of the buffered boardwalks, although the area of the boardwalks only encompassed 26% of the total study area (192 ha of 726 ha).

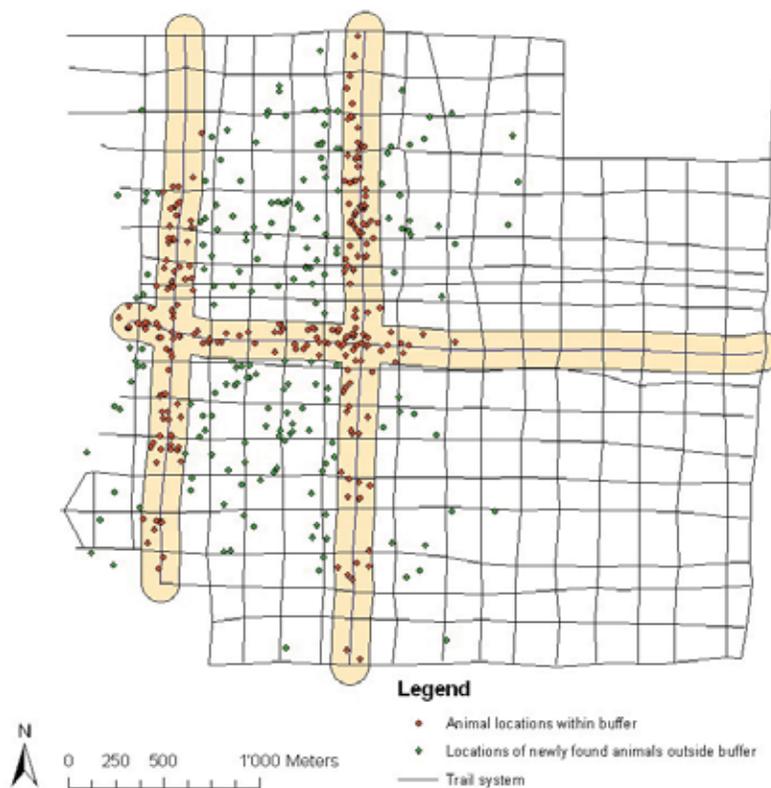


Fig. 26 Locations of newly found animals in- and outside the buffer around the boardwalks. Note: there are no observations in the eastern part of the study area because this part has only recently been added.

This indicates a strong encounter bias due to the boardwalks. However, as the animal is followed from the point where it was encountered, the observation bias of boardwalks was not present anymore if all observation points were used. For this dataset, 30.98% of all locations lay within the buffer (12'493 of 40'331 locations). There was thus no observation bias found for the major boardwalks.

#### 2.4.10 Effect of autocorrelation on home range sizes

For all four individuals autocorrelation was significant, according to both Swihart & Slade as well as Schoener's index for sample sizes  $\geq 50$ . For one female (Jinak) data was significantly autocorrelated for the 25 location sample as well. This indicates that autocorrelation is present in the orangutan data especially at large sample sizes as was to be expected due to the sampling procedure. Table 7 shows that autocorrelation indices increase with increasing sample sizes if all observations are used to take subsamples from.

Juni		
N = 4666	Swihart & Slade index	Schoener's index
Sample size	Value > 0.6 indicates significant autocorrelation	Value < 1.6 or > 2.4 indicates significant autocorrelation
25	0.5232	1.8168
50	0.7496	1.3706
100	1.4552	0.9607
500	2.1911	0.3730
1000	2.3170	0.2099
2000	2.4882	0.1076

Tab. 7 Both indices indicate significant autocorrelation for sample size  $\geq 50$  for all observations.

If only night nests are used and time steps between successive observations were larger than 24 hours, autocorrelation was still present in the data, but only for sample sizes larger than 100. Indices of autocorrelation at the same sample size were smaller if only the nest location data was used to draw the sample from than when all location data was used (table 8).

Juni		
	Swihart & Slade Index	Schoener's Index
Sample size		
25	0.3889	2.5468
50	0.7923	1.4708
100	1.2818	1.0830

Tab. 8 Values of autocorrelation if only nest locations (time step  $\geq 24$ hrs) were used

Home ranges calculated with the more autocorrelated samples yielded larger home ranges (301.79 ha  $\pm$  118.00, n = 12) than ranges calculated with less autocorrelated or independent locations (278.09 ha  $\pm$  90.87, n = 12), but differences were not significant (Mann-Whitney U, Z = -0.404, p > 0.05). There was thus no effect of autocorrelation on range size estimates found.

## 2.5 Discussion

### 2.5.1 GPS measurement error

GPS devices are a powerful tool for collecting location data of wildlife. Often mentioned constraints of telemetry location data (Moser & Garton 2007; 1249, White & Garrot 1990: 41-75) do not apply to manually collected GPS locations of animals in sight. However, the GPS-device used to determine locations of individual orangutans may be prone to measurement-error itself. Several studies suggest that GPS measurement error is dependent on satellite geometry, terrain and habitat type (Cain et al. 2005, DeCesare et al. 2005, Sager-Fradkin et al. 2007). The question addressed concerning GPS measurement error was how large the GPS location error was at the Tuanan field site.

Mean GPS location error was less than 10 meters and is thus comparatively low for a tropical forest. Results for GPS measurement error from a study in mountainous terrain with coniferous forest gave similar errors as were reported in this study: 95% of locations were within 17.7 metres of predefined reference-coordinates (Sager-Fradkin et al. 2007: 1303) whereas in this study, 95% were within 18 metres. Wing and Eklund (2007: 9) on the contrary reported higher measurement accuracy of 7.2 m for GPS data collected under dense canopy cover.

Apart from satellite geometry, terrain and vegetation cover, the GPS device itself might also influence measurement accuracy. Whereas some ten years previously, researchers had found recreational, hand-held GPS devices to be of no use in primatological field studies due to problems of location accuracy in tropical forests (Phillips et al. 1998: 167), data from Tuanan suggests that this view has to be revised. However, the degraded peat swamp forest at Tuanan cannot be compared to a primary tropical rainforest in terms of tree height and canopy cover. Canopy height at Tuanan is estimated to be around 15-20 meters, as compared to a height in primary tropical forests of around 30 meters (Sutton et al. 1983: 4-6). In the study area there are also always at least some areas with patches of daylight on the forest floor, which indicates an incomplete canopy cover. These factors taken together can account for the comparatively low location error in Tuanan. The reported measurement errors are comparatively small and do not hinder data collection with GPS in any way.

### Effect of canopy cover

The effect of canopy cover could not be tested directly, as no objective measurement of canopy density was possible (e.g. with a spherical densitometer as in Phillips et al. 1998: 169). An approximation used was to compare location error in camp (no canopy) with location error within the forest. The means for the two locations differed significantly, but location error was higher in camp than in the forest. One possible explanation for this could be that although there is no canopy cover in camp, the obstruction of several small buildings in camp had a larger effect on GPS signal interference than canopy cover. No effect was found for the factor "rain" on GPS location error. This is in accordance with the theory of GPS radio signals that are broadcasted with low frequencies to minimize the effects of weather phenomenon such as clouds or rain. However, although GPS signals can transverse through leaves, signals are easily diminished by liquid water e.g. when foliage is wet (Patton 2008, online, accessed 21.4.2008). So the effect of rain should only be noticeable in the forest when leaves are wet, i.e. after it has rained. However, field experience showed that very heavy rainfalls during a rainstorm effectively blocked out all signals and made localisation impossible, even in camp. Although no effect of rain on location error within the forest could be demonstrated, it can not be completely excluded.

### Satellite geometry

An exploratory review of satellite geometry for the Tuanan location confirmed the anecdotal evidence that getting location fixes in the afternoon is more difficult than in the morning. Around mid-day, only 4 satellites are visible, some of them at low elevations, so that their signals might easily be blocked by trees. However, duration of bad satellite availability is less than one hour. The experience in the field showed that getting a first position fix was always possible, but took longer in the afternoon. In this case a suggestion would be to turn on the GPS in the morning before searching or following, as the GPS has less difficulties of updating a position with bad satellite coverage than to acquire a new position 3 kilometres away from the last fix. To further improve the accuracy of GPS data, only three-dimensional fixes should be recorded, as they have a smaller location error. Guidelines for observers and researchers on how to collect GPS data can further improve data acquisition with GPS. For suggested guidelines for GPS data acquisition see Annex 2. Accuracy of GPS collected positions was found to be sufficient for collecting orangutan location data.

### **2.5.2 Comparison of two field methods**

A comparison of the two field methods showed that the manual mapping yielded fairly accurate results. The formulated research question which method of field data collection performed better could thus not be answered definitely. It has to be taken into account that manual maps go through a process of “double-manual-mapping” (once on the paper map and once in the GIS) that could be very error-prone. This was not the case for the analysed follows and both methods gave useful results. However, if the two methods are evaluated in terms of effort, GPS data collection will certainly outperform the manual mapping and very time-consuming digitalization. On the other hand, the advantage of drawing maps is that the process is not dependent on functioning GPS devices, batteries, satellite availability etc. Spatial and behavioural data is recorded separately in both manual data collection and GPS recording. Thus, attribute synchronisation is an obstacle in both methods, unless focal data would also be recorded digitally (e.g. with handheld PDA's). Both field data collection methods have their strengths and weaknesses. In conclusion, the GPS data collection is less observer-dependent, less time-consuming and will in general also be more accurate than manual mapping. When starting GPS data collection it is important that a standard data collection protocol is followed and that problems that could arise (such as measurement errors, position acquisition difficulties, coordinate format and data integration into a GIS) are assessed beforehand in order to avoid delays and problems later on. If these conditions are met, use of hand-held Global Positioning System (GPS) devices in the field offers a time-saving alternative to the tiresome manual digitalization of paper maps.

### **2.5.3 Choice of home range model**

Choosing an appropriate home range model is important to accurately depict animal space use and to understand the ecological processes that affect animal movements. The lack of consistent criteria to select a home range model suited for a specific data set has long been lamented. Horne & Garton (2006: 1147) were the first to present a framework for objective model selection using the “information-theoretic approach” that enables determining the relative support from the data for a given model. The question addressed in this study was how the model selection could be optimized using objective criteria.

Results of model comparisons using the likelihood-cross validation criterion as an approximation of the Kullback-Leibler distance indicate that fixed and adaptive kernels are both good models for estimating home ranges compared to bivariate normal distributions. Despite its increased complexity, adaptive kernel did not always outperform fixed kernel. With increasing sample size, deviation from the “true” model also increased in both bivariate normal and adaptive kernel. Assumed underlying distributions – except kernels – represent hypotheses about animal home range use. The bivariate normal distribution for example

approximates the space use of an animal that wanders out equally in all directions but continually returns to a central place (Horne & Garton 2006: 1151). This assumption was clearly not met for orangutan distribution data as the difference in likelihood-cross-validation criterions ( $\Delta\text{CVC}$ ) increased with sample size, indicating that the bivariate normal distribution is not supported by the data. When estimating home ranges for orangutans, in accordance with the information-theoretic approach, either fixed or adaptive kernels should be used as home range models. Fixed kernel performed slightly better than adaptive kernels for all individuals, but especially for one female (Mindy) where only the fixed kernel model was selected. The fixed kernel model thus had the best support from the real spatio-temporal orangutan data set and was therefore selected. The superior fit of fixed over adaptive kernel implies that no differential smoothing is necessary because the animals visit most parts of their range repeatedly over time. As orangutans do not have a central place they return to (such as a permanent nest or den) no areas of high location density occur that would need to be more smoothed than infrequently used ones.

#### **2.5.4 Performance of minimum convex polygon method**

Although the minimum convex polygon method has been shown to have several severe methodical shortcomings (Burgman 2003: 27), it is still used, most often in combination with other models (Laver & Kelly 2008: 293). Kernohan et al. (2001: 138) found that minimum convex polygon method requires more than 100 fixes, often 200-300, to obtain reliable estimates of home range size. This behaviour of the minimum convex polygon method was confirmed for the Tuanan orangutan data. However, even larger sample sizes than the recommended 200 - 300 locations were required to reach stable home range estimates. Sometimes no asymptote was reached even with as many as 2000 location points. Increase in home range estimates was steeper at small sample sizes and less pronounced with larger sample sizes. This can be explained by the fact that with few observations, any additional observations are likely to lie outside the already defined convex hull, whereas with many observations, only few are likely to lie outside and will thus add to the size of the convex hull. The recommendations of minimum required sample size made by Harris et al. (1990 in Kernohan et al. 2001: 138) should be modified, depending on the animal studied and the sampling scheme applied. In this study, sample sizes of at least 500 points from the overall point data set of each animal were needed to reach asymptotic home range sizes with the MCP method. Other commonly cited disadvantages of the MCP method are that it assumes uniform range use within the convex hull, is unable to account for multiple centres of activity, relies on outlying points as points of the convex hull, and may include large unused areas (Katajisto & Moilanen 2006: 406).

Researchers have tried to solve these problems by excluding outlying points with various methods. However, these “point-peeling-techniques” only exclude points without any biological rationale. The advantage of the MCP method was said to be its comparability between studies, which is often a problem for the new state-of-the-art methods such as kernels (Laver & Kelly 2008: 290). Therefore, it was suggested that every study should use two home range estimators, of which one is the MCP method (Harris et al. 1990 in Kernohan et al 2001: 139). Kernohan et al. (2001: 140) disagreed because comparisons will be unreliable due to the methods’ sensitivity to sample size and sensitivity to outliers. However, applying two home range estimators was adopted in many studies (for recent examples of publications e.g. Moyer et al. 2007, Molinari-Jobin et al. 2007, Wilson et al. 2008).

The various constraints of the MCP method have led the scientific community to mostly abandon the MCP method as a home range size estimator. The findings of the previous analysis support this consensus. I believe that the use of the MCP method in wildlife biology and ecology as a home range size estimator has little future. Even for comparisons across studies the focus should lie on devising reliable guidelines and standards for the more sophisticated methods.

### **2.5.5 Performance of kernel estimation methods**

Kernel methods are used as a standard for estimating home ranges. The problem is that a large variety of smoothing factors, kernels and sample sizes leads to a bewildering number of possible combinations for the kernel method (Gitzen et al. 2006: 1342) , each possibly producing quite divergent home range size estimates. Each decision for a kernel, smoothing factor or sample size needs to be reflected and has to be justified, as it will influence home range size estimates. As to the choice of kernel method (adaptive or fixed), the information-theoretic approach already suggested the use of fixed kernel. Furthermore, a preliminary inspection of results for different sample sizes and smoothing parameters showed that adaptive kernel oversmooths the utilization distribution and overestimates home range size by including more infrequently used areas. However, a comparison of difference in mean home range sizes between the two methods was not significant. Horne and Garton (2006b: 644) pointed out that the choice of smoothing parameter has an important influence on estimating distributions. In their study on smoothing parameter selection for fixed kernel, Gitzen et al. (2006: 1334) showed that no method performed well for all distributions. Rather, choice of bandwidth selection method should vary according to study goals, sample sizes and patterns of space use exhibited by the species studied.

### Smoothing parameter selection

The performance of three common smoothing parameter selection methods was compared (Least-Squares Cross-Validation, Biased Cross-Validation and  $h_{\text{reference}}$  method). Hemson et al. (2003: 458) reported failing to compute LSCV at sample sizes larger than 300 and failure in 99% of cases at 550 points. LSCV estimates were also very variable for orangutan data and failed to compute at sample sizes larger than 100. Therefore, using the LSCV method can not be recommended for orangutan data where sample sizes for individuals can be large and we do not necessarily want to apply rigorous subsampling. The relatively novel method of BCV was tested and compared against LSCV and  $h_{\text{reference}}$  method. It performed well for all sample sizes and was less variable than LSCV. BCV was chosen as an objective method to select smoothing parameters as it strikes a balance between over- and undersmoothing and is robust also at large sample sizes. Because there is such high variability depending on smoothing factors, studies estimating home ranges should take this into account and make an explanatory analysis to the sensitivity of their home range estimates to varying smoothing parameter selection methods.

### Sample size in kernel estimations

Sample sizes of at least 30 independent locations were recommended for kernel estimates as a representative sample. Kernohan et al. (2001: 138) recommended that 50 or more samples should be collected for each study period, e.g. if seasonal and yearly home ranges are evaluated, 30-50 points should be used for every season. This assumption was tested and sensitivity of home range size estimates to sample size assessed to answer the question how home range size estimates varied with sample size.

For all females, range increase from  $n = 25$  to  $n = 2000$  varied from 37% to 71% when  $h$  was held constant. Although asymptotes were reached for all four individuals, the problem of holding  $h$  constant is that it will undersmooth locations at low sample sizes. This leads to discontinuous home ranges at small sample sizes. At larger sample sizes,  $h = 0.3$  will oversmooth the distribution and overestimate home range size. Selecting the same smoothing parameter for different sample sizes can not be recommended. Rather, an objective method to select smoothing parameters should be identified and used, such as the BCV method. However, when BCV was used to select smoothing parameters range estimates decreased with increasing sample sizes. Based on the findings of this study, sample sizes of 200 – 500 locations are recommended for home range estimates in orangutans. With fewer locations, variation due to random subsampling might be large. The 'optimal' sample size that was assumed to lie between 100 and 500 locations, as home range size increases up to 100 locations and thereafter slightly decreases. A sample size of 300 locations per individual was selected for this study as this sample size minimized

deviations from the mean home range estimates. However, as variation according to sample size was small and differences were not significant, other sample sizes may also be used, provided that samples are drawn from a larger pool of data (e.g. out of a total of 4000 observations or 2000 observation hours).

These recommended sample sizes for orangutans are considerably larger than for other species (e.g. 10 fixes per month for roe deer (*Capreolus capreolus*) and kestrel (*Falco tinnunculus*) in Börger et al. 2006: 1402). This indicates that orangutans as arboreal mammals with slow locomotion need comparatively longer to traverse their home range than other, more mobile species such as birds. Using 200 - 500 consecutive points per animal which equals 100 - 250 follow hours will probably not give an appropriate estimate of an orangutan's space use pattern. In practice, unequal sample sizes are commonly attained for different individuals which leads to problems in subsequent comparisons between individuals. It has been advised against aggregating data collected over different time intervals to get the same number of locations, as this may lead to problems in the following statistical analysis. Börger et al. (2006: 1401) demonstrated that the common advice of standardizing the number of fixes (e.g. Seaman et al. 1999) is not sufficient to obtain unbiased statistical inferences from data, as the response to variation in sampling regime may differ between the years. Pooling data collected over varying time intervals in order to obtain an equal number of fixes may lead to misleading statistical results, as the variation in home range size estimates depended more on the number of days sampled than on the total number of fixes. This has obvious implications for comparative analyses, namely that the sampling regimes should be standardized. This will ensure that inferences are robust to sampling variation in the number of fixes without having to pool data over different time intervals.

### **2.5.6 Comparing home range estimates**

In order to make meaningful comparisons, estimating home ranges with equal sample size could offer a solution, but will not entirely solve the problem of variation in home range size estimates. Therefore it was tested whether differences between individuals were more pronounced than differences between models and sample sizes to answer the question of what influence method and different parameters had on home range estimates.

If the same model was used, individual differences were significant, whereas differences between sample sizes were not. This supports previous findings (Börger et al. 2006: 1401) that individual features of space use will cause a larger variation in home range size than differences in estimation method. However, this only holds true if estimation methods are similar. This finding was contradicted if home range models with different assumptions are used, such as kernels and convex hulls. Range estimates from kernel methods differed

significantly from results of MCP method. Therefore, comparisons across studies are only valuable if similar models were used. As the MCP method performed poorly compared to the kernel estimations, it is highly recommended to use kernel estimates in future home range studies. Börger et al. (2006: 1401) also indicate that methodological analyses based on real animal location data but with low numbers of individuals should be treated with caution. Results of such studies could be influenced by idiosyncratic patterns and may not show a general trend. They thus advise that once a threshold number of fixes per unit time is collected, effort should be put into collecting data of more individuals. However, for primatological field studies the main objective is usually to collect behavioural data and large sample sizes are required for the same individual. Spatio-temporal data is collected as a “side-product” and can thus not “dictate” the sampling strategy for field data collection, however desirable the sampling of more different individuals might be.

### **2.5.7 Effect of observation bias**

Current home range models implicitly assume equal probabilities of obtaining locations across an individual's home range. However, most GPS telemetry studies reported marked differences in these probabilities. It was hypothesized that other methods of data collection, e.g. also hand-held GPS data collection will be biased as well. This assumption was tested for orangutan location data in Tuanan. For the newly found animals an encounter bias in locations was found. The area along the boardwalks encompassed more locations of newly encountered animals than the rest of the study area, which points towards a severe encounter bias. However, if all locations are taken into account, this observation bias noticeably decreases and percentages of observations relative to the area where they were collected are nearly equal. If orangutans were searched and only one location per animal per day would be recorded (namely the place where it was found) this would induce a strong observation bias into the location data and the resulting utilization distribution estimates. However, due to the nature of the study site at Tuanan with flat terrain and homogeneous forest and because animals are followed for long time periods, observation bias should not be a concern to researchers working with orangutan data from Tuanan and similar study sites.

### **2.5.8 Effect of autocorrelation**

Another often discussed issue in animal home range studies is the effect of autocorrelation on range estimates. When dealing with autocorrelation in home range studies it is important to highlight the sensitivity of different models to dependent data. In their study, de Solla et al. (1999) compared home ranges estimated of turtles and antler flies with differing amounts of autocorrelation using kernel methods. They found that bias in home

range estimates was reduced when more autocorrelated data was used. They never achieved completely independent data by subsampling locations while maintaining an adequate sample size for kernel estimates. They thus concluded: "*Much of the autocorrelation present, particularly at the longer time intervals, is likely to be an intrinsic property of home range behaviour*" (de Solla et al. 1999: 228-229). Their study showed that serial independence is not a prerequisite when working with kernel density estimators and that autocorrelated data may be even necessary to adequately model animal movements.

Kernohan et al. (2001: 130) concluded that an adequate sampling of animals during the study period is more important than finding a time interval between subsequent observations that is statistically independent. They advised on designing a sampling schedule that takes into account the behavioural features of the animal studied. For example, movements of nocturnal animals should also be sampled adequately at night. For orangutans, this is not a problem as they are diurnal and usually spend the night sleeping in their nests. Furthermore, the duration of the study period in Tuanan is sufficiently large to take into account the different aspects of daily and seasonal movements. The applied sampling strategy generates data that are useful for home range studies, although the frequent sampling of locations (every 30 minutes) will introduce autocorrelation into the dataset. Autocorrelation was still present in data even when only nest locations are used, which is in accordance with the hypothesis by Swihart and Slade (1985: 1183) that time to independence will be larger than 24 hours for non-territorial primates. Again, this is linked to the motion patterns of female orangutans and indicates that a time span of one day is not enough to achieve temporal or spatial independence of observations. However, if only independent locations are used for home range estimates and the time to independence is larger than one day, the sample size needed for a stable and reliable estimate will not be met.

The question whether autocorrelation is a problem for orangutan range estimates can be answered in the negative. With less autocorrelated data, home range areas estimated with kernel density were smaller than with more autocorrelated data. However, as differences were small and not significant, it can be concluded that autocorrelation does not have an important effect on home range estimates for orangutan data. Therefore, I value considerations of adequate sample sizes higher than issues of autocorrelation and do not advocate rigorous subsampling or exclusive use of nest locations in an attempt to reduce or eliminate autocorrelation.

### 3. Fruiting seasonality and orangutan ranging behaviour

#### 3.1 Introduction

After having resolved many of the underlying issues associated with data and model uncertainties, the analysis of orangutan ranging behaviour should yield results that are not influenced by methodological errors but represent the unbiased biological phenomena.

Ranging behaviour in mammals is influenced by different factors; one of the most important is food availability. As preferred foods such as fruit become scarce, animals can attempt to maintain a constant daily energy intake by exploiting fruit patches more thoroughly or by travelling more to visit different patches. As abundance of preferred foods continues to decline, full compensation becomes increasingly difficult. Animals may migrate to a different habitat where fruit abundance is higher, a strategy called “area switch”. The area switch is expected to occur in habitats that encompass a variety of different micro-habitats or altitudinal ranges and is more likely to be adapted by flying frugivores such as birds and bats. The second response was proposed to be more common among primates: they may switch to other foods that yield less energy per unit consumed but also need less travel (and less energy) to be exploited. Such food items are termed “fallback foods” and include for example young leaves (van Schaik & Brockman 2005: 6-7). For orangutans it has been shown that ranging and habitat changes coincide with periods of food abundance rather than scarcity (Hemingway & Bynum 2005: 77). Sumatran orangutans were observed to follow the production of fruits along altitudinal bands in their home ranges (Buij et al. 2002: 83).

For Bornean orangutans, Leighton & Leighton (1983: 188-189) observed changes in rates of sightings of orangutans that were at least in part related to changing food abundance. During periods of high fruit abundance, more orangutans were observed along transects, especially non-resident, sub-adult males. When food became scarce, those individuals emigrated from the area. The findings of seasonal movements of non-residents are also supported for Sumatra by Te Boekhorst et al. (1990: 1098) who reported that non-residents of both sexes were equally attracted to the study area when food was abundant. However, as Leighton & Leighton (1983) only observed orangutans from transects, they were unable to report home range changes or changes in daily travelled distances for resident females or males. Furthermore, generally less is known on the seasonal ranging patterns of orangutans in Borneo than in Sumatra. The goal of this study is to close this gap by providing quantitative measures for orangutan ranging behaviour in relation to seasonality for a peat swamp forest in Central Kalimantan.

The key question addressed was: *What is the relationship between seasonality in the environment and changes in ranging behaviour of female orangutans?*

More explicitly, the following questions were addressed and the respective assumptions tested:

*a.) Do home ranges of resident female orangutans remain stable over years?*

The hypothesis was that orangutans in Tuanan maintain stable home ranges over several years. Because the habitat grain is too coarse, no habitat that is in a phenologically different state is available at close distance that would render a habitat switch profitable.

*b.) How does the degree of interactions between individuals vary seasonally? Is the spatial tolerance between individuals different depending on whether food is abundant or scarce?*

Theoretically, tolerance among individual females should be higher when food is abundant, and ranges are expected to overlap more in the fruiting period, when benefits of association might outweigh costs. During fruit scarcity, individuals may avoid encounters and retreat to their core areas, thereby reducing range overlap with other individuals.

*c.) Do female orangutans change their ranging behaviour during times of food scarcity or abundance?*

Although home ranges may remain relatively stable over years, it was hypothesized that seasonal changes in fruit abundance could result in different foraging strategies. If the strategy followed is to minimize energy-expenditure, ranges are expected to decrease. On the other hand, if orangutans aim at maximizing their net-energy-intake, seasonal ranges are expected to increase, as distances between different patches of high-energy food sources increases.

*d.) How is the search behaviour affected by seasonality? Do orangutans range more during periods of fruit scarcity or during fruit abundance?*

During periods of high fruit abundance, orangutans are expected to range more and cover larger distances in order to maximize their energy-intake by visiting fruit trees in different patches. This behaviour should be reflected in increasing daily travelling distance. During periods of fruit scarcity, orangutans are presumed to minimize energy expenditure and therefore decrease travelled distances.

In this study, only ranging data of females was analysed. The reason for this is twofold: First and foremost, subadult and adult males use range of at least 2500 hectares and perhaps even much more (Singleton & van Schaik 2001: 877). Due to the unfeasibility of collecting location data with radio-transmitters or GPS-collars in orangutans, location data is collected by direct observation of focal animals. The quantity of spatial data for orangutans

males that occupy large home ranges is thus much reduced compared to females. Furthermore, there is an ongoing debate whether male orangutans are attracted by receptive females. The support for this hypothesis has been mixed, as Te Boekhorst et al. (1990) suggested that the number of non-resident males that temporarily visit an area was more correlated to food availability than the number of reproductive females. Utami (2000) on the contrary showed that number of reproductive females correlated positively with the number of flanged males in Ketambe, Sumatra in some years. Singleton et al. (in press: 206) conclude that we may safely assume that male range use is largely a response to the distribution of females in orangutans, as in most other mammals. Ranging responses to fluctuations in fruit availability can therefore be more confidently drawn from orangutan females than males.

Summarising, primates often face marked changes in the availability of their major food types (Hemingway & Bynum 2005: 58) and need to react accordingly. Those reactions often encompass a spatial component. Even if the strategy of an area switch is not the primary option for the sedentary orangutans, a diet switch might also show a spatial component because fallback foods are less aggregated than fruits and would thus need less travelling time and distance to be exploited. Therefore, behavioural changes may also emerge as spatio-temporal patterns that can be analysed and used to draw conclusions from.

## 3.2 Methods

### 3.2.1 Calculating annual and seasonal ranges

To assess whether ranges remained stable over years for female orangutans, annual ranges were calculated for five females (Jinak, Juni, Kerry, Mindy, Sumi) starting in 2003 to 2007. A total of more than 22'000 observation points was used. As every point equals 30 minutes of observation, this results in roughly 11'000 hours of observation used in the analysis. Observation hours between individuals varied greatly, the minimum observation hours used were 200 hours for Kerry in 2004 whereas the maximum was 1030 observation hours for Mindy in 2005. Because of insufficient sample size, Sumi's range was only calculated from 2004 onwards. Sumi died in August 2006 and no range was calculated for that year.

The method to define the annual range was fixed kernel density estimation as implemented in the ArcGIS (ESRI) Extension Home Range Tools by Rodgers et al. (2007). As variance in x and y coordinates was unequal, they were automatically rescaled with a unit variance before smoothing parameter selection was applied. Biased-Cross validation was used as the method to select smoothing parameters. The default raster resolution size of 150m for kernel contours was used, as lower values would have substantially increased calculation time. Range sizes reported are based on 90% volume contours. This procedure was arrived at based on a detailed study in the first part of this thesis (see chapters 2.4 and 2.5).

To assess whether ranges remained stable over several years, for each individual overlaps between consecutive years were calculated as the intersection between the two annual ranges (based on 90% volume contours). The percentage of the overlap area of the previous annual range area is a measurement of site fidelity. It answers the question: *How much of last year's range is contained in the following year's range?* The formal definition of stable home ranges used was that at least half of the previous years' range had to be contained in the following year's range.

However, the overlap between two consecutive years does not convey any information on whether annual ranges gradually shift or stay stable over several years. To account for the possibility of shifting ranges, a matrix was calculated with overlaps between all possible sampled years (e.g. 2003 with 2004, 2005, 2006 etc.) for every individual.

As different amounts of total observation hours were used as a data pool to draw the subsamples from, a test was needed to check for influence of observation effort on range estimates. Spearman's correlation was used (SPSS 14.0) to test for correlation of observation effort and range estimates.

The calculation of seasonal ranges was similar to that of annual home ranges, except that the time scale chosen was seasons defined by fruit availability rather than calendar years. Seasonal ranges calculated with less than 300 location points were not included in the statistical analysis.

To account for the intensity of interaction overlaps were calculated both for the 90% volume contour (overall range) and for the 50% volume contour (core range with higher intensity of use). Overlaps were calculated in ArcGIS 9.2 (ESRI) as the intersection of the respective range polygons.

In order to assess orangutan space use for several years and to compare home ranges with other studies, home ranges were calculated for the entire study period. Four females that were repeatedly followed from 2003 to 2007 (Jinak, Juni, Kerry, Mindy) were selected. Home ranges with kernel methods were calculated as described above (random selection of 300 points). For kernel home ranges, 95% and 90% volume contours are reported. In addition, minimum convex polygons were calculated based on the entire point group for a female, but with 95% and 90% of points selected by the floating mean method as described in chapter 2.3.3.

### **3.2.2 Defining fruiting seasons according to phenology**

Phenology is the science of the study of the periodic biological phenomena such as the fluctuations in the productions of fruits and flowers (Brearley et al. 2007: 828). Thus, phenology is an ideal indicator of seasonal changes in the vegetation. In a phenology plot, 1611 numbered trees have been surveyed every month since 2003 to assess productivity of the forest. As an index of habitat wide fruit abundance, the Fruit Availability Index (FAI) was used.

$$FAI = \text{number of trees carrying fruit} / \text{total number of trees in the plot}$$

The FAI indicates the percentage of trees in a plot that carry fruit in a specific month. Estimates of number of fruits per tree were reclassified to binary values (whether a tree was carrying fruit or not). Estimating number of fruit a tree carries is highly subjective and therefore observer-dependent, an effect that could be reduced by only using binary data. Another option would have been to calculate an edible fruit abundance index which is based on observations of fruit orangutans had consumed during the study period. However, both indices have been shown to be strongly correlated (pers. comm. N. Zweifel) and the seasonal patterns do not show major differences to the availability index including all species (Haag 2007: 17), see also figure 27.

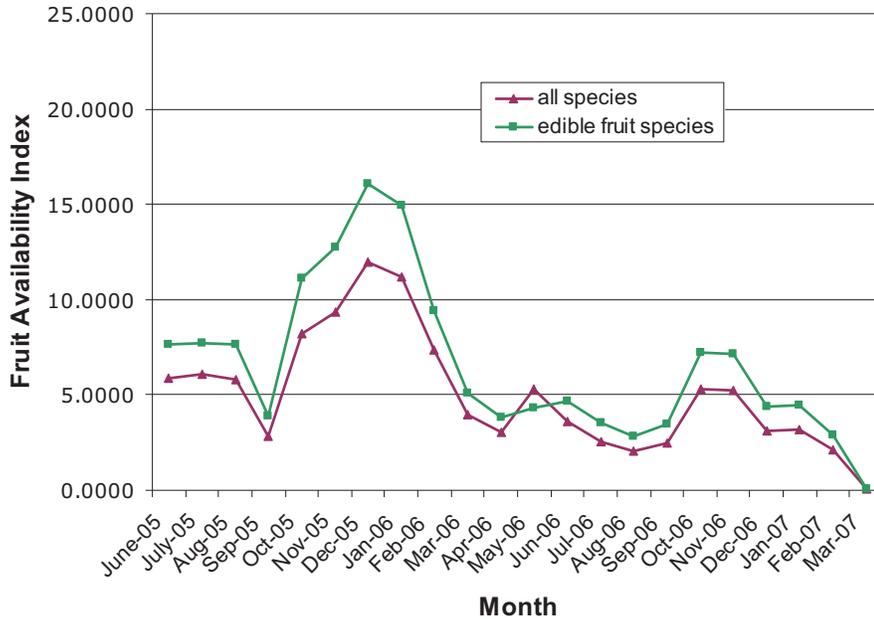


Fig. 27 Edible fruit availability compared to fruit availability of all species (edible fruit data courtesy of N. Zweifel, Anthropological Institute and Museum, University of Zurich, Switzerland).

Habitat-wide fruit availability was used to define two seasons in Tuanan: A period of low to medium fruit abundance indicating food scarcity and a period of high fruit availability, indicating food abundance. The monthly FAI values were automatically classified into three classes using quantiles. The three classes of FAI are as follows:

Low Fruit Availability	0.0656 - 3.1475
Medium Fruit Availability	3.1475 - 6.0904
High Fruit Availability	6.0904 – 13.9855

Tab. 9: Classification of fruit availability

Using the average FAI value as a break to define two classes was not deemed suitable, as too many months would have been classified as months with sufficient fruit availability for orangutans, although they were intermediate. The two classes of low to medium fruit availability were later aggregated to one class in order to calculate seasonal ranges for continuous periods. All three classes were retained for analysis of travelling distances. At the time of the study, the phenology data was available until November 2007.

### 3.2.3 Computational motion analysis

The calculation of daily travelled paths and distances between consecutive nests yields important information on animal space use which complements and extends the analysis of annual and seasonal ranges. Daily travelled paths (also referred to as daily travel distance) is defined as the total distance an individual orangutan travels per day, from the moment it leaves it's nest in the morning to the moment it builds it's next night nest. In this study, daily

travelled paths are approximated by summing the distance between half-hour locations. Nest distance is defined as the minimum direct distance between two consecutive night nests.

#### Problem statement

Given the large amount of orangutan location data that has been collected so far, a manual approach of data analysis is only feasible as long as the time frame for analysis remains large (e.g. years or seasons) and the amount of calculations small. If the time scale is reduced to “motion windows” of days or even hours, the amount of data processing needed increases rapidly and soon exceeds the time frame of any master theses many times over. Hawthorne Beyer, developer of “Hawth’s Tools” extension for ArcGIS remarks: *“The benefit of a software solution is that it can be conveniently repeated, and that the analysis (which often involves numerous intermediate stages) is consistent, streamlined, documented, fast, and easily adapted or modified.”* (<http://www.spatial ecology.com/>, accessed 21.7.2008). Large amounts of spatial data such as the daily movement patterns of orangutans that need to be analysed in a repetitive manner call for a computerised approach.

So far the problem has been tackled either manually with rolling a map-distance-meter on the paper maps or in ArcGIS by selecting days and individuals and performing analysis step by step. However, with increasing data volumes, these approaches become infeasible. Therefore, an automated approach was needed to process the existing data and to perform the repeated calculation of nest to nest distance, daily travelled path and distances between subsequent observations. The programming language chosen to develop such a software solution for the aforementioned problem was the object-oriented Java programming language. Design steps followed during development were adapted from Arnow & Weiss et al. (2004). The following section provides a short overview of how the program was designed and implemented.

#### Primary objects, behaviour and interactions

The data used by the java program was based on the follow maps digitized in ArcGIS. The attribute table contained information on date and time of each half-hour observation point as well as the name of the individual and additional information such as species of a feeding tree or if the point was a nest or not. UTM coordinates were added to the attribute table using the “add x/y-coordinates” tool implemented in ArcGIS. This attribute table was exported as a tab-delimited text-file that could be read in by the java program. Thus, a class was needed to handle the reading-in of the data. The class “DataLoader” reads in the data from the text file and creates new objects if needed. The basic functionality of the DataLoader class was adopted from a term project on spatial algorithms (Faes & Wartmann 2008, unpublished).

The geographic coordinates are stored in a “Location” class that inherits from the Java Point2D class. It represents the locations where orangutans were observed with their UTM coordinates and stores the information whether the point was a nest or not. Geometric analyses such as calculating turning angles between successive steps are handled in the Location class. The class “Observation” has a Location object and stores additional information such as the time of the observation and remarks. The class “Lifeline” represents one orangutan day from morning nest to night nest. All observations with identical follow number are added to a Vector <Observation> that contains only objects of the class Observation. The Lifeline class is able to perform analyses such as calculating the total daily travelled distance and nest to nest distances. To ensure that only complete follows were used, a static method “*sortLifelines*” sorts all Lifelines. After that, it can be tested whether the lifeline starts and ends with a nest location. If this is not the case, a static method called “*removeIncompleteFollows*” removes these follows from the data to be analysed. The class Individual represents an orangutan and stores its name, sex and age. Every Individual-object has another Individual-object called “infant” as a class variable that represents its offspring. All lifeline objects are eventually added to their respective individual-object. A diagram of the class-design can be found in figure 28. In summary, the program represents individual orangutans. Every orangutan “knows” where it was, at which day and at which time. In this context “to know” means to store the particular data needed to answer this question and to provide the methods to retrieve them.

### Functionality

The program functionality was amply tested and several adaptations were incorporated. Among them was the implementation of a method that tests every lifeline for double observations. If by mistake an observation is added to the GIS-map twice, with the same time and date but with a slightly different location, values for speed are disproportionately exaggerated (e.g. speeds of 160m/s). To avoid such outliers influencing subsequent statistical analysis, the method *removeDoubleObservations* tests for double observations and removes them from the Vector. Over 1000 double observations (from a total of more than 40'000) were identified by the aforementioned method and were permanently removed from the database to avoid problems in future studies.

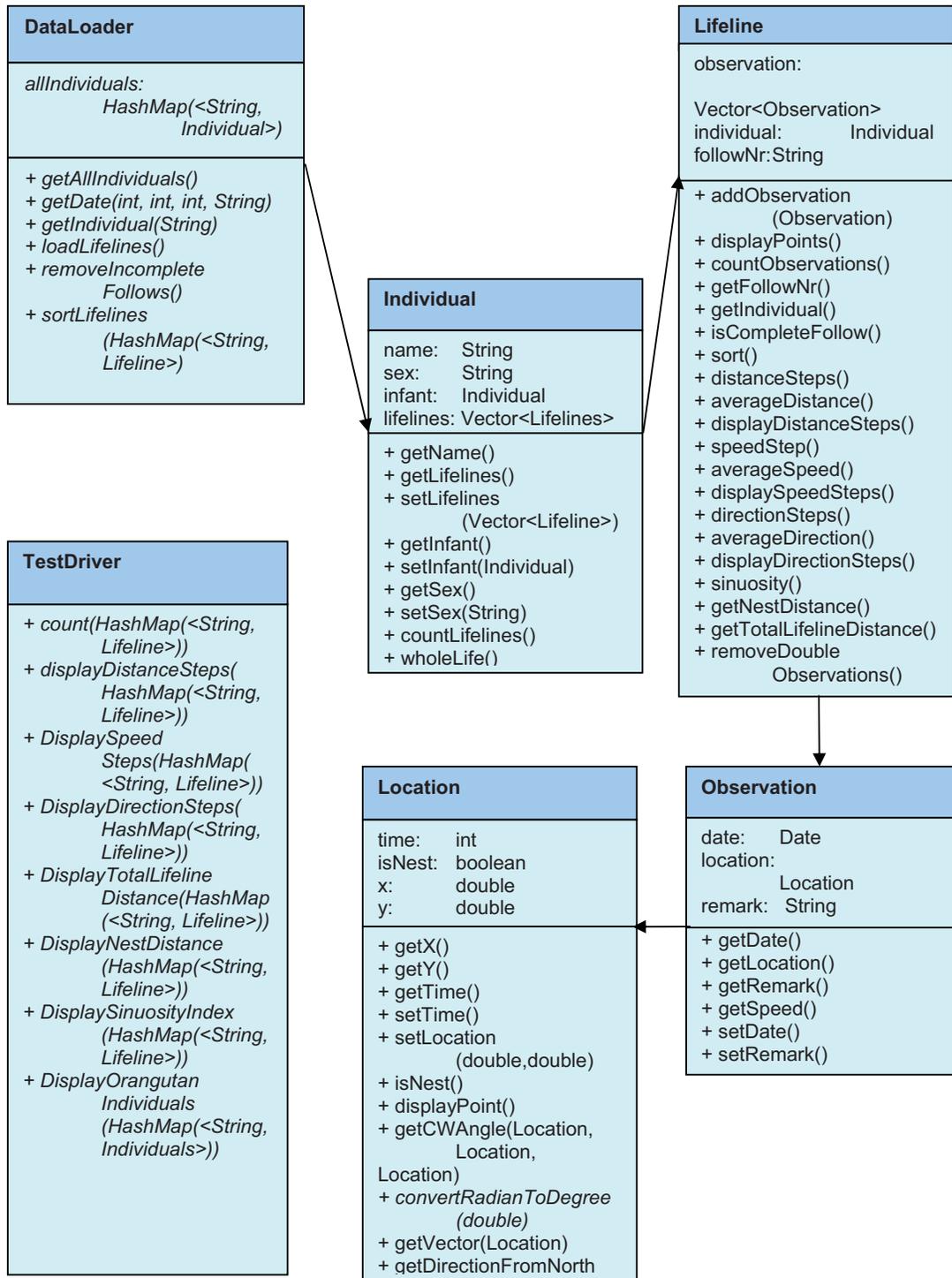


Fig. 28 Class diagram of Java program

### 3.2.4 Calculating feeding time and active period

Data on orangutan activity budgets and diet has been collected by various researchers, students and assistants since beginning of the orangutan study project in Tuanan. Data from focal sheets are entered into an access-database from where they can be processed and extracted.

For this study, feeding times were calculated for two different groups: “fruit” and “vegetative matter”. Information on feeding times is collected by behavioural researchers in “bouts” of two minutes. Number of feeding bouts was thus multiplied by 2 to obtain feeding time in minutes. All feeding bouts of flowers, immature or mature fruit were classified as “fruit-feeding”, whereas young and old leaves, stems, pith and bark were grouped as “vegetative matter feeding”. Insects and other invertebrate food items were not included in the analysis, as the feeding time spent on those items is comparatively low (6.3% of total feeding time in Tuanan, Morrogh-Bernard in press: 124). Although flowers, unripe and ripe fruits may differ in their energetic content, they were grouped into a single class as their seasonal availability in space and time was hypothesised to significantly influence ranging of female orangutans, as opposed to vegetative matter much of which is more or less available all year round.

### 3.2.5 Defining reproductive state and age of offspring

Age of dependent and semi-independent offspring as well as sexual reproductive state of females were taken into account to analyse influence of these factors on ranging. Age estimates of immatures were done by Carel van Schaik and Serge Wich, both experienced orangutan researchers, when they first encountered the individuals. Dunkel (2006: 15) made some adjustments to these age estimates using facial morphology and comparisons between infants with known ages (see tab. 10).

Mother	Infant	Birth of Infant	Age of Infant in 2008
Jinak	Jerry	estimated May 03	5
Juni	Jip	Feb 06	2
Kerry	Kondor	estimated 1999	weaned, 9
Kerry	Kino	Jan 07	1
Mindy	Milo	estimated 2nd half 2001	weaned, 7
Sumi	Susi	estimated 2nd half 2002	died
Desy	Deri	June 2004	4

Tab. 10 Orangutan mothers and their infants

Reproductive states of females were grouped into two categories: sexually active and not sexually active. Periods of sexual activity for females were defined when they engaged in voluntary matings and were observed in association with males. During the study period, two females were sexually active, namely Juni (from beginning of 2004 to August 2005) and Kerry (from beginning of 2003 to April 2005 and from November 2005 to May 2006).

### **3.2.6 Statistical analysis**

Data were analysed in SPSS v. 14.0 (SPSS Inc., Chicago). For a comparison of means, Analysis of Variance (ANOVA) was used if data were normally distributed. For non-normally distributed data, Mann-Whitney-U's test was used for comparing two groups and Kruskal-Wallis's test for comparing three or more groups. Each factor or variable was analysed for individual and seasonal differences. Furthermore, all variables that might explain variance of daily travelled distance were included in one model to account for interactions between variables and assess the relative importance of the different variables. A univariate analysis of variance was performed to determine which factors were best able to explain or predict the dependent variable "total daily travel distance". Variables were transformed using the natural logarithm to better fit the assumption of normality. Variables transformed were total daily travel distance, nest distance, vegetative matter feeding time and sinuosity index.

### 3.3. Results

#### 3.3.1 Annual ranges and core areas

During the course of any year, female orangutans in Tuanan used an area of approximately 200 ha (90% contour). Differences in range size between years were not significant (Kruskal-Wallis, Chi-Square = 1.934,  $p > 0.05$ ). Of all females, Juni had the largest range size with 298 ha ( $\pm 0.94$ ) whereas Mindy occupied the smallest range (128 ha  $\pm 0.22$ ). For values of all female home ranges see figure 29. Mean differences in annual range size between two consecutive years were very small for Kerry, Mindy and Sumi (between 14% and 15%). For Jinak and Juni they were higher with an average range size difference of 38% and 39% respectively, indicating higher variability and fluctuations. Size of annual home ranges did not differ between years (Kruskal-Wallis, Chi-Square = 1.719,  $p > 0.05$ ) but they were significantly different between individuals (Kruskal-Wallis, Chi-Square = 11.213,  $p < 0.05$ ).

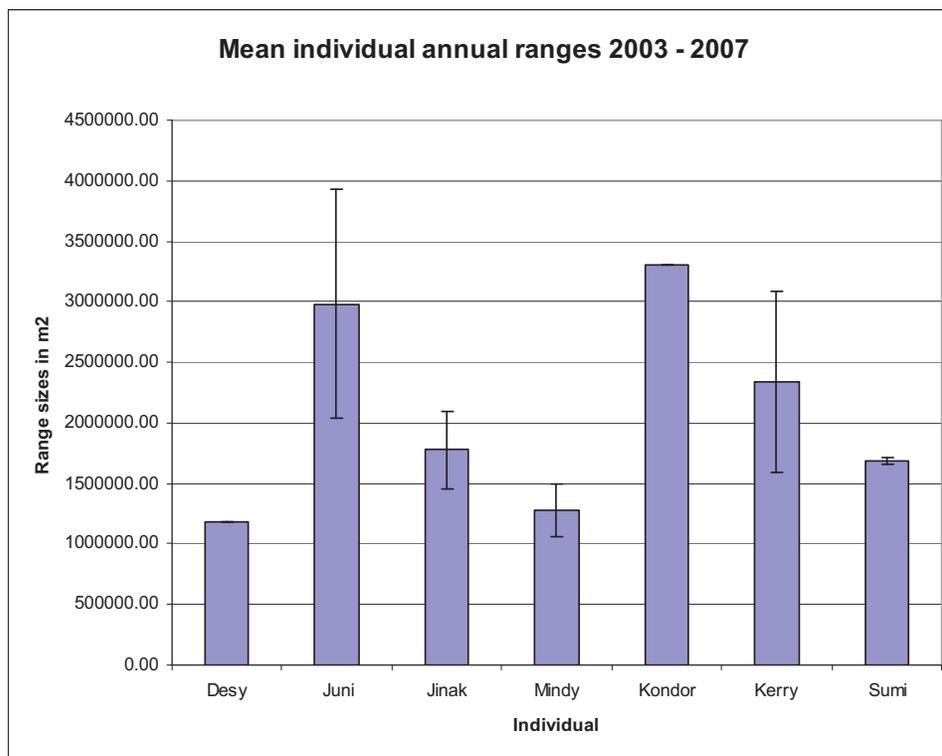


Fig. 29 Mean individual annual ranges from 2003 to 2007

Spearman's correlation showed no effect of total observation effort on annual area estimates (Spearman's rho = 0.13,  $p > 0.05$ ). Core areas were on average 65 hectares large, amounting to 33% of the annual range. During half the time, female orangutans thus occupied only a third of their range. However, annual range and core area sizes alone do not necessarily convey a complete picture of orangutan ranging over the years.

### 3.3.2 Range overlaps for the same individual between years

Range overlaps for the same individual between different years fill this gap as they show which parts of the range were used over two or more consecutive years. Average range overlap (calculated as the percentage of range in year 1 contained in range in year 2) was 76.38% ( $\pm 13.19$ ). This confirms that home ranges of adult female orangutans in Tuanan remain relatively stable over several years.

Overlaps within the same individual between different years were considerably higher than overlaps between any two individuals ( $39\% \pm 21$ ). The female Mindy showed the highest site-fidelity with a mean overlap of 84% between two consecutive years, whereas Kerry had the smallest range overlap with 71% overlap on average. Sumi was excluded as only one comparison was possible. An example of a decreasing range, and therefore small overlap was Juni. In 2005, Juni occupied an area of 450 ha that decreased to an annual range of 240 ha in 2006, which results in an overlap of 52%.

Although overlap between individuals in annual ranges was on average higher than 30%, areas of higher use overlapped considerably less, as can be seen in the visualisation in Annex 5. This indicates that females use the same areas over time, but that intensively used areas are more exclusively used.

### 3.3.3 Home ranges for the entire study period

To facilitate comparisons with studies from other sites where home ranges were calculated for the entire study period, ranges are also reported based on all collected point location data from 2003 to 2007 for each female (see figure 30 and table 11).

Individual	Kernel 0.95	Kernel 0.9	Total Nr. of Points
Juni	379.31	313.06	5535
Kerry	440.64	350.98	2213
Mindy	216.87	169.84	6709
Jinak	239.82	194.45	7183
Mean	<b>319.16</b>	<b>257.08</b>	

Tab. 11 Home ranges in ha for the study period (year 2003 - 2007)

Note that the overlaps in figure 30 do not contain any information on time, e.g. whether the overlapping areas were used by the females at the same time or at different times.

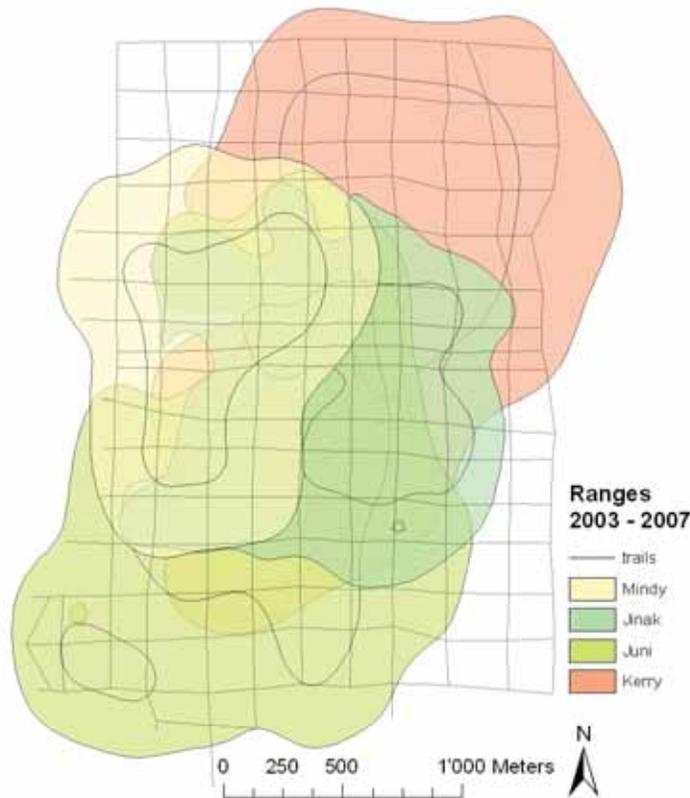


Fig. 30 Ranges for the entire study period 2003 – 2007

Even if home ranges are estimated for the entire study period, a substantial individual variation in home range sizes remains, e.g. with Mindy consistently having the smallest ranges of all females. Total observation effort did not have a direct influence on range estimates, as Mindy with 6709 locations as the second most observed female had smallest ranges of all females studied (see table 11).

### 3.3.4 Seasonality in fruit availability

If ranging pattern is only analysed at the temporal scale of years, important details of spatio-temporal range use might be lost. Therefore it is necessary that ranging be analysed at a finer temporal granularity. As orangutans are a primarily frugivorous species, using fruiting seasons provides a meaningful measure of intra-annual ranging differences. Using the Fruit Availability Index (FAI) to analyse seasonal patterns of fruit abundance, it can be seen that fruits peak in the wet season, usually around December (figure 31).

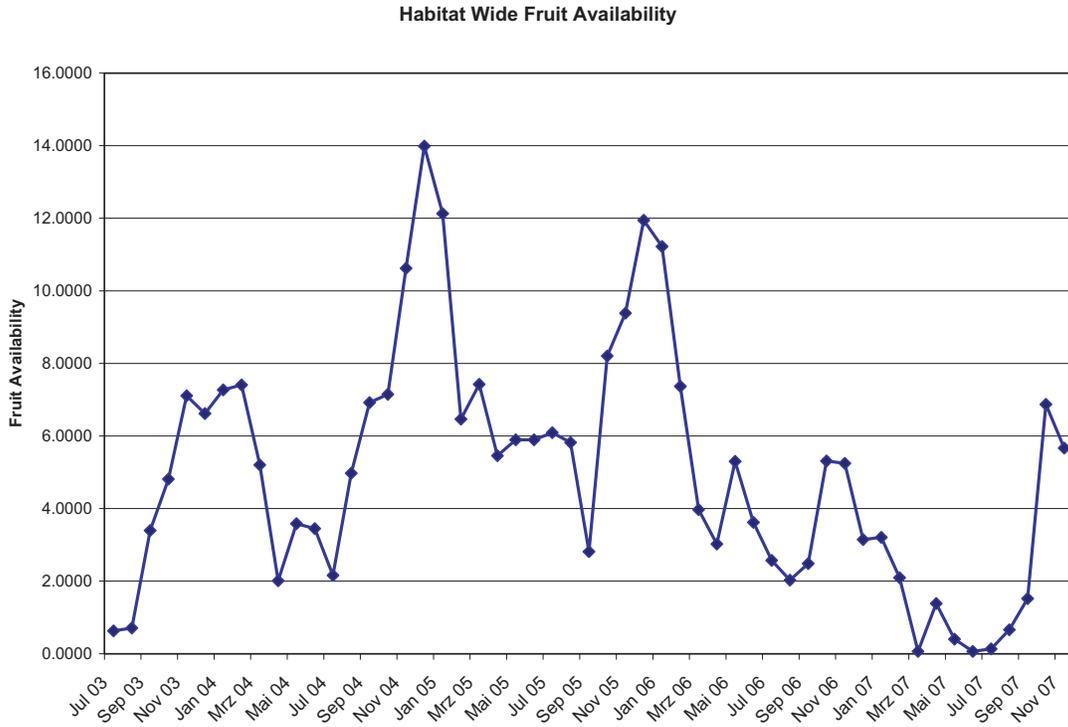
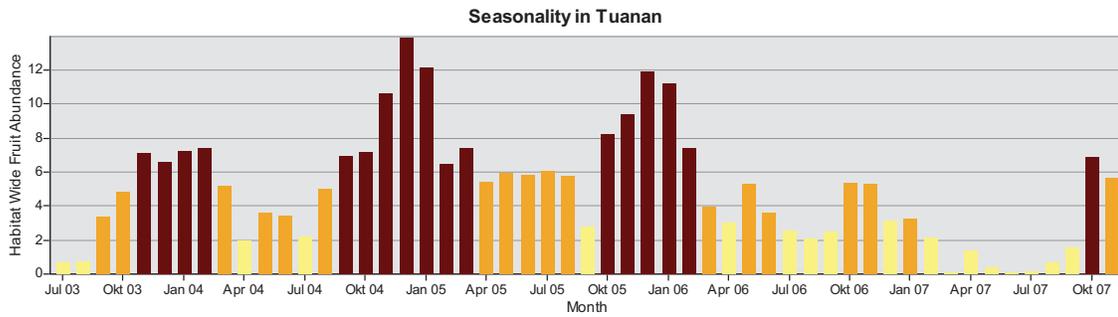


Fig. 31 Habitat Wide Fruit Availability (FAI) at Tuanan



**Legend**

- Low Fruit Availability: 0.065600 - 3.147500
- ◐ Medium Fruit Availability: 3.147501 - 6.090400
- High Fruit Availability: 6.090401 - 13.985500

Fig. 32: Classification of seasons for Tuanan

The classification of months according to fruit availability (figure 32) resulted in the following definition of seasons for Tuanan:

Season / duration	Months
<b>Food abundance</b> 4 months 7 months 5 months (2 months)	November 2003 – February 2004 September 2004 – March 2005 October 2005 – February 2006 October 2007 – November 2007 (not included in analysis)
<b>Food scarcity</b> 4 months 6 months 6 months (19 months) → subgroups: 6 months 6 months 7 months	July 2003 – October 2003 March 2004 – August 2004 April 2005 – September 2005 March 2006 – September 2007 (division into three subgroups) March 2006 – August 2006 September 2006 – February 2007 March 2007 – September 2007

Tab. 12: Classification of seasonality in fruit availability

### 3.3.5 Seasonal ranges

Mean range size for individuals was smaller when fruit was abundant (158 ha  $\pm$  0.58) than when it was scarce (197 ha  $\pm$  0.85). However, differences in range size between the two seasons were not significant (Mann-Whitney U, Z = -1.703, sig. 2-tailed p > 0.05). Core ranges were slightly larger in the abundant season (63.37 ha  $\pm$  28.9) than in the lean season (53.14 ha  $\pm$  20.6) but differences were again not significant (Mann-Whitney U, Z = -1.443, sig. 2-tailed p > 0.05). The seasonal range sizes varied more between individuals than between seasons. Differences between individuals in seasonal ranges were significant (Kruskal-Wallis, Chi-Square 17.656, p < 0.05), as well as in seasonal core areas (Kruskal-Wallis, Chi-Square 16.102, p < 0.05). Individual idiosyncrasies are thus superimposed on seasonal ranging patterns - if present.

Seasonal range sizes or core areas did not correlate significantly with total sample size per individual (Spearman's rho, correlation coefficient = 0.1 and 0.181, respectively, both p > 0.05). Seasonal range size and core areas also did not correlate with the duration of the respective seasons in months (Spearman's rho, correlation coefficient = 0.099 and 0.104, respectively, both p > 0.05). Thus, any differences among seasons recorded here are not artefacts of differential sampling.

### 3.3.6 Seasonality of range sharing

As a measure of habitat sharing and probability of interaction, overlaps of outer and inner range boundaries (90% and 50% volume contours) were calculated between all individuals for the two different seasons. The highest overlap observed was found for Mindy, with 99.93% of Mindy's home range being contained in Jinak's home range. On average,  $39\% \pm 21$  of any individuals' home range were contained in any other individuals' range. The females sharing more than a quarter of her home range with another female were Jinak ( $48\% \pm 21$ ), Mindy ( $46\% \pm 23$ ) and Sumi ( $42\% \pm 23$ ). Juni and Kerry shared approximately a third of their home range with another female ( $32\% \pm 16$  and  $31\% \pm 20$ , respectively). Differences between individuals were significant (Kruskal-Wallis, Chi-Square 17.572,  $p < 0.05$ ). Home range overlap was higher when fruit were scarce ( $72.98 \text{ ha} \pm 41.29$ ,  $n = 45$ ) than when they were abundant ( $60.43 \text{ ha} \pm 33.36$ ,  $n = 26$ ), but differences were not significant (ANOVA,  $F = 1.740$ ,  $p > 0.05$ ). However, differences between individuals were significant (ANOVA,  $F = 4.403$ ,  $p < 0.05$ ).

Core range overlaps were consequently a lot smaller than home range overlap, with an average of  $11.8\% (\pm 17.1, n = 136)$ , with few exceptions. The highest core area overlap was observed for the two females Juni and Jinak in 2003, where Jinak had 84.7% of her core area contained in Juni's core range. Differences between individuals in core range overlap were not significant (Mann-Whitney U,  $Z = -0.669$ ,  $p > 0.05$ ). Core range overlap was larger when fruit were scarce ( $13.3\% \pm 18.1$ ) than when they were abundant ( $9.52\% \pm 13.6$ ), but not significantly (Kruskal-Wallis, Chi-Square 0.729,  $p > 0.05$ ).

### 3.3.7 Seasonality in daily movement

For further analyses a different temporal window was chosen that captures the motion patterns of orangutans in more detail. Rather than choosing seasons defined as sequences of several months, the temporal scale chosen was the day divided into motion steps by subsequent 30 minutes observations. The basic elements that can be used to describe motion from point A to point B are distance and speed. Distance and speed were analysed both for differences between individuals and between seasons.

#### Speed

Female orangutans travelled on average with a speed of 0.023 meters per second (m/s) ( $\pm 0.012$ ,  $n = 971$ ) which translates to approximately 82 meters per hour. As these are daily averages which may also include long feeding and resting periods, maximum obtained speeds of orangutan females may be considerably larger.

Of all females, Kondor travelled fastest with 0.032 m/s ( $\pm 0.017$ ,  $n = 69$ ) on average. The slowest individuals were Jinak ( $0.019 \text{ m/s} \pm 0.009$ ,  $n = 239$ ) and Desy ( $0.017 \text{ m/s} \pm 0.040$ ,  $n$

= 509). Differences in speed between individuals were significant (Kruskal-Wallis, Chi-Square 85.201,  $p < 0.05$ ). During months with low FAI, orangutan females travelled at a slower pace ( $0.022 \text{ m/s} \pm 0.011$ ,  $n = 393$ ) than in months with medium FAI ( $0.0231 \pm 0.013$ ,  $n = 297$ ) and high FAI ( $0.0235 \pm 0.011$ ,  $n = 281$ ). Differences between seasons were not significant (Kruskal-Wallis, Chi-Square = 5.319,  $p > 0.05$ ). Individual differences in average travel speed were thus more pronounced than seasonal differences.

#### Nest distance

Distances between morning and night nest on the same day were measured as the direct line between the two nests. On average, orangutan females in Tuanan built their night nest 413 meters from the morning nest away ( $\pm 220.58$ ,  $n = 972$ ). Significant individual differences between nest distances were observed.

Individual	Mean	N	Std. Deviation
Desy	278.64	22	187.83
Jinak	375.52	239	172.68
Juni	484.83	163	284.54
Kerry	477.88	144	225.95
Kondor	408.11	69	211.11
Mindy	415.48	194	215.53
Sumi	353.06	141	175.40
Total	413.85	972	220.58

Tab. 13 Distances between morning and night nest for individuals

Juni's night nests were spaced farthest away from all analysed individuals with an average of 484.83 m ( $\pm 284.54$ ,  $n = 163$ ). The individual with the closest nest distances was Desy with 278.64 m ( $\pm 187.83$ ,  $n = 22$ ), but note the small sample size compared to other females. Differences between individuals in nest distances were significant (Kruskal-Wallis, Chi-Square = 42.523,  $p < 0.05$ ).

seasons	Nest distance	N	Std. Deviation
low FAI	376.08	393	202.63
medium FAI	431.03	296	231.49
high FAI	450.38	281	224.76
Total	414.38	970	220.40

Tab. 14 Seasonal differences in nest distance

During months of low fruit availability, nest distances were on average 376.08 metres ( $\pm 202.63$ ,  $n = 393$ ), during months of medium fruit availability 430.64 ( $\pm 231.204$ ,  $n = 297$ ) and during high fruit availability 448.82 ( $\pm 225.89$ ,  $n = 282$ ).

Differences of nest distance between the three seasons were significant (Kruskal-Wallis, Chi-Square = 22.857,  $p < 0.05$ ). Nest distances correlated weakly, but significantly with the Fruit Availability Index (Spearman's rho, correlation coefficient = 0.195, sig. 2-tailed  $p < 0.05$ ).

### Total daily travelled distances

As nest distances only contain information on how much distance orangutans covered between their sleeping places, total daily movement paths reveal more information on what distances were actually travelled per day. On average, an orangutan female in Tuanan travelled 777 meters per day ( $\pm 402.39$ ,  $n = 972$ ). The subadult female Kondor had the longest daily path lengths of all studied females ( $954.07 \text{ m} \pm 474.92$ ,  $n = 69$ ) and topped her mother Kerry ( $847.73 \text{ m} \pm 445.23$ ,  $n = 144$ ) in total daily path length. The female Desy had the shortest day path lengths with  $474.10 \text{ metres} (\pm 320.27, n = 22)$ . Differences between individuals were significant (Kruskal-Wallis, Chi-Square 59.655,  $p < 0.05$ ).

Individual	Mean	N	Std. Deviation
Desy	474.10	22	330.27
Jinak	678.24	239	322.35
Juni	835.85	163	450.90
Kerry	847.73	144	445.23
Kondor	952.07	69	474.92
Mindy	848.04	194	405.35
Sumi	669.44	141	286.72
Total	777.21	972	402.39

Tab. 15 Total daily travel distances for orangutan females

Total daily travel path lengths also correlated positively with Fruit Availability Index (Spearman's rho, correlation coefficient = 0.225,  $p < 0.05$ ), indicating that the more fruit are available, the more distance orangutan travel during the day. With low fruit availability, mean daily travelled distance was  $694.80 \text{ meters} (\pm 348.49, n = 393)$ . In months with medium fruit availability, distances were on average  $822.04 \text{ meters} (\pm 456.85, n = 297)$ . In months with high fruit availability, distances travelled per day were largest with  $844.84 \text{ meters} (\pm 392.46, n = 282)$ . Differences between the three seasons were significant (Kruskal-Wallis, Chi-Square 33.780,  $p < 0.05$ ). Daily travelled path length correlated significantly with nest distance (Spearman's rho, correlation coefficient = 0.701, sig. 2-tailed  $p < 0.05$ ).

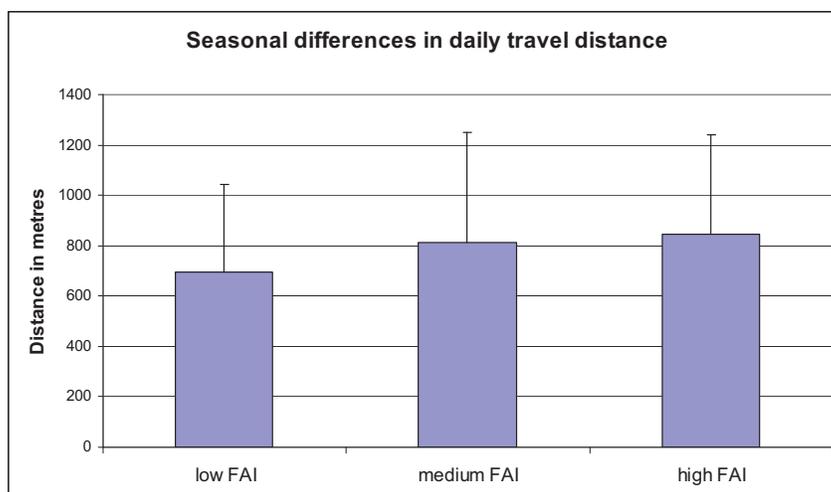


Fig. 33 Seasonal differences in daily travel distance

## Sinuosity Index

Bringing the two spatial measurements of nest distance and daily travelled path lengths together is the objective of the sinuosity index. It reveals the relationship between nest distances (the minimal distance) and how far an orangutan actually travelled during the day. The larger the daily travelled path and the smaller the nest distance, the higher the sinuosity index. High values thus indicate long day paths and small nest distances; small values stand for little difference between nest distance and path lengths.

The mean sinuosity index evaluated at the time scale of a follow day for all females was 2.17 ( $\pm$  1.54,  $n = 971$ ). Females thus covered on average twice the distance in their actual travel path than the distance between their nests.

Seasonal differences in sinuosity index were less pronounced than individual differences. In the season with lowest fruit availability, the daily sinuosity-index was lowest with 2.133 ( $\pm$  1.40,  $n = 393$ ). It was highest during months with medium fruit availability (2.23  $\pm$  1.86). During high fruit availability it was intermediate (2.156  $\pm$  281,  $n = 297$ ). Differences between the seasons were not significant (Kruskal-Wallis, Chi-Square 0.360,  $p > 0.05$ ). The sinuosity-index did not correlate with fruit availability (Spearman's rho, Correlation coefficient = - 0.001,  $p > 0.05$ ).

Individual	Mean	N	Std. Deviation
Jinak	2.0955	239	1.3782
Juni	2.0640	163	2.0212
Kerry	1.8483	144	0.6595
Kondor	2.5812	69	1.1170
Mindy	2.4056	193	1.8000
Sumi	2.2767	141	1.6233
Desy	1.8640	22	0.6804
Total	2.1708	971	1.5418

Tab. 16 Sinuosity Index for orangutan females

Individuals that travelled less than twice the distance between nests were Kerry (1.85) and Desy (1.86). Highest sinuosity indexes were found for Kondor with 2.58 and Mindy with 2.41. Differences in sinuosity index between individuals were significant (Kruskal-Wallis, Chi-Square 41.963,  $p < 0.05$ ).

An example of a high sinuosity index can be seen in figure 34. On this day (9.2.2006) Mindy travelled a total distance of 1708 metres. The distance between the morning and the night nest was only 189 metres, which results in a sinuosity index of 9.02 for that day.

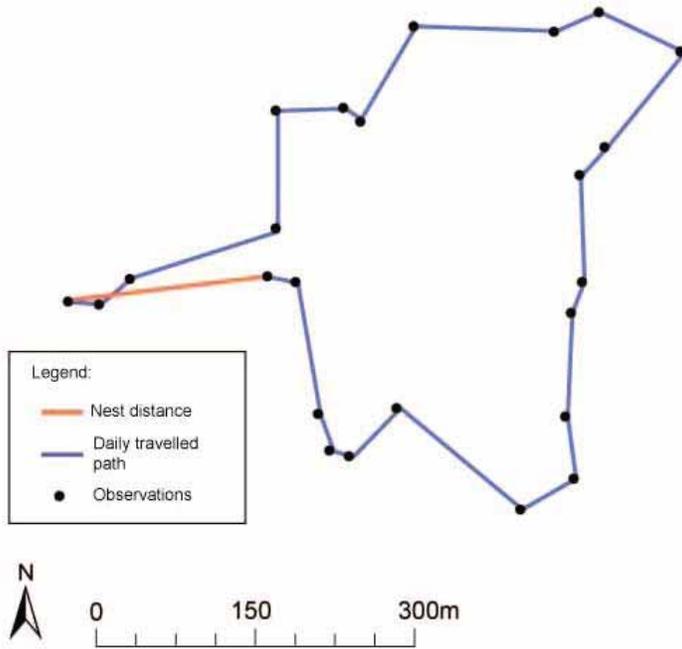


Fig. 34 Example of a spatial pattern that results in high sinuosity index of 9.02

### 3.3.8 Who's who in the “hutan”: Ranging results of individual orangutan females

#### Jinak

Jinak is one of the older females in the study area. The birth of her infant Jerry was estimated to have taken place in May 2003, before beginning of observations. Another female in the study area, Juni, presumably also is her offspring, an assumption that has recently been confirmed by genetic analyses. Jinak's home range and core area were largest in 2004 (226.41 ha and 77.89 ha respectively) and smallest in 2005 (131.37 ha and 48.64 ha). On average, Jinak occupied an annual range of 177.52 ha ( $\pm 31.89$ ).

Jinak	seasons		Day path length	Nest distance
	low FAI	Mean	626.66	380.44
		N	73	73
		Std. Deviation	258.55	168.19
	medium FAI	Mean	666.40	356.68
		N	93	93
		Std. Deviation	396.06	174.06
	high FAI	Mean	744.89	394.61
		N	73	73
		Std. Deviation	262.32	175.27

Tab. 17 Jinak's daily motion results

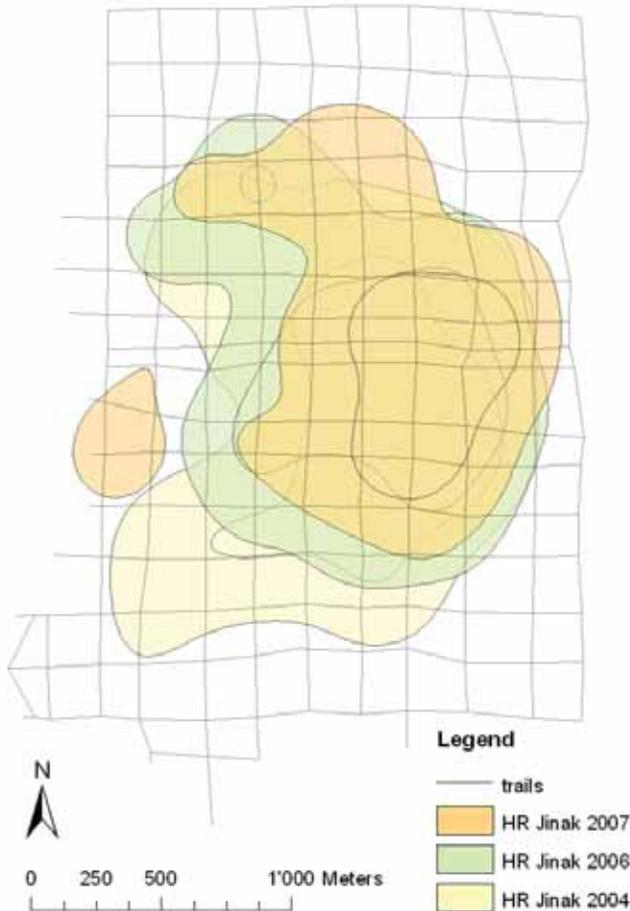


Fig. 35 Jinak's annual ranges

Her daily ranging followed a seasonal pattern. During periods of low fruit availability, Jinak travelled least (626 m) and the sinuosity index (1.86) was also lowest in this season. When fruit were available on a medium basis, she increased her daily travel path to 666 metres. When fruit were abundant, daily travel path and nest distance were largest (745 and 395 metres respectively), as well as the sinuosity index (2.24). Length of daily travel paths differed significantly between seasons (Kruskal-Wallis, Chi-Square 12.062,  $p < 0.05$ ), but nest distances did not (Kruskal-Wallis, Chi-Square 2.282,  $p > 0.05$ ), see also Annex 3.1.

### Juni

One of the younger females in the area, Juni gave birth to her first infant Jip in February 2006. Juni is thought to be Jinak's daughter, an assumption supported by the fact that from July to October 2003, 95% of Jinak's home range was also contained in Juni's range. Juni had one of the largest average home ranges of the females studied. In 2004 and 2005 when she was actively searching out males for matings she occupied ranges of 358 and 452 hectares respectively. After giving birth to Jip, her range decreased by 46% to 244 hectares

in 2006. In the year 2007, when fruit availability was generally very low and Juni was still lactating, her range further decreased to 186 hectares with a core area of 58 hectares. During months of low fruit availability Juni had the shortest day path length (739 m). Juni had the largest sinuosity index during medium fruit availability (2.69) as well as the longest day journey length (955 m). During months of high fruit availability she had the lowest sinuosity index (1.65). When fruit were abundant nest distance was longest (565 m). Differences between the three seasons were significant for sinuosity index, nest and daily travelled distance (Annex 3.2).

Juni	seasons		Day path length	Nest distance
	low FAI	Mean	739.00	413.21
		N	78	78
		Std. Deviation	411.80	235.48
	medium FAI	Mean	955.18	534.14
		N	41	41
		Std. Deviation	398.36	317.48
	high FAI	Mean	896.33	565.82
		N	44	44
		Std. Deviation	529.46	306.00

Tab. 18 Juni's daily motion results

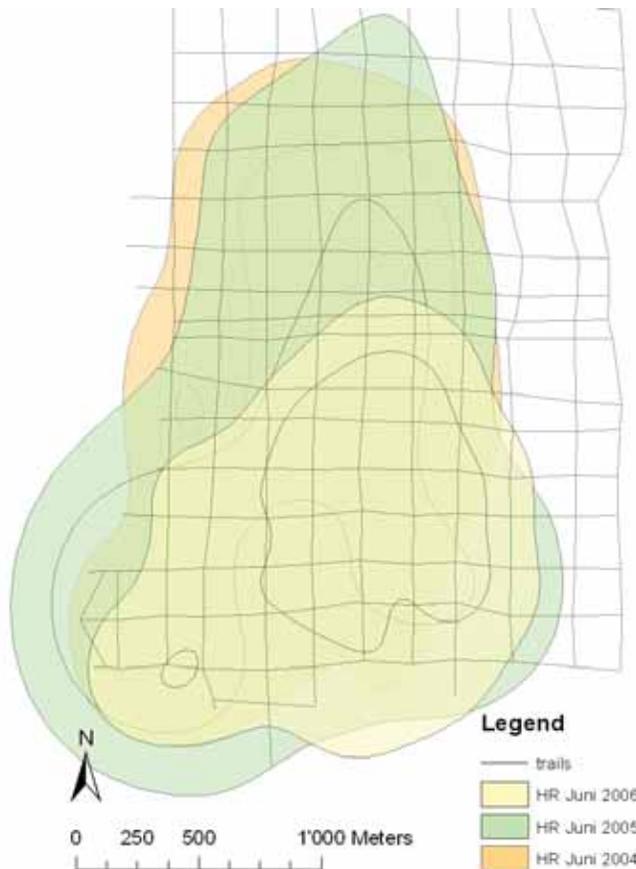


Fig. 36 Juni's annual ranges

## Kerry

Kerry is the mother of two known orangutans in the study area: Kondor, a sub-adult female estimated to have been born in 1999 and Kino, an infant born in January 2007. Kerry, also one of the females with larger home range areas (233 hectares on average) started off with a range of 126 hectares in 2003 when her first infant Kerry was about 4 years old. Over the years her range increased and in 2007 she occupied the largest range since beginning of observations (330 hectares home range and 101 ha core area).

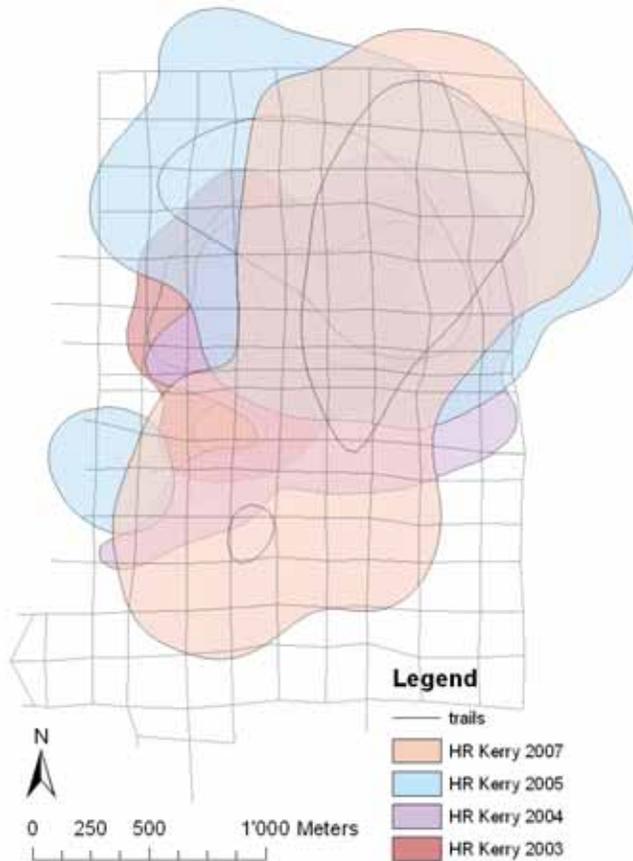


Fig. 37 Kerry's annual home ranges

Kerry had the shortest day path length (657 m), nest distance (386 m) and sinuosity index (1.78) during months of low fruit availability. During months of medium fruit availability daily travelled distance was on average 1025 metres and nest distance was 557 metres. When fruit were abundant she travelled 977 metres per day and her night nests were on average 546 metres apart. Differences between the three seasons were statistically significant for daily travel distance and nest distance (Annex 3.3).

Kerry	seasons		Day path length	Nest distance
	low FAI	Mean	657.26	386.79
		N	65	65
		Std. Deviation	333.29	196.06
	medium FAI	Mean	1025.91	557.55
		N	44	44
		Std. Deviation	494.94	239.23
	high FAI	Mean	977.46	546.89
		N	35	35
		Std. Deviation	432.52	202.50

Tab. 19 Kerry's daily motion results

### Kondor

The sub-adult female Kondor, offspring of Kerry had an estimated age of 9 years in 2008. Kondor was weaned in 2005 and has since then lived a semi-independent life, in proximity of her mother Kerry. Due to sampling requirements, Kondor's range could only be calculated for 2007. In this year, Kondor occupied an annual range of 330 hectares and a core area of 101 hectares (figure 38).

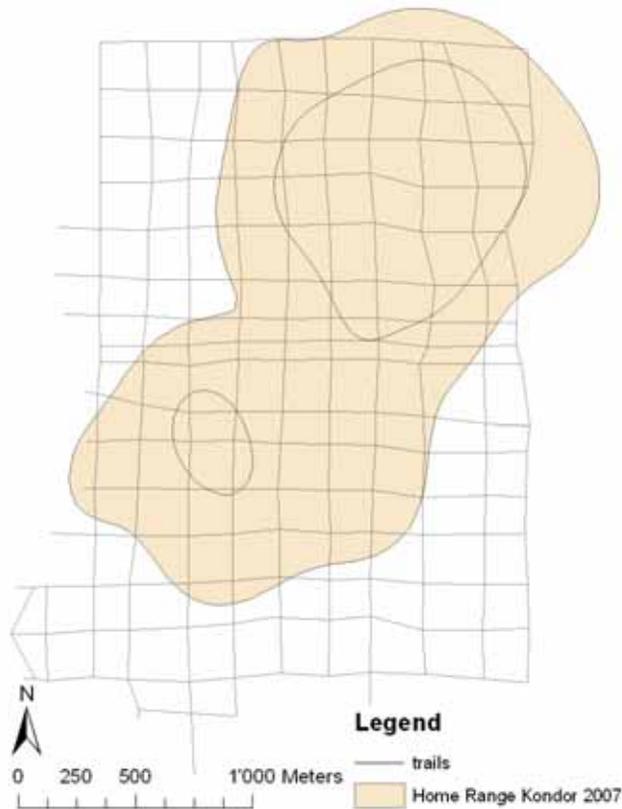


Fig. 38 Kondor's Home Range in 2007

Kondor	seasons		Day path length	Nest distance
	low FAI	Mean	827.85	367.66
		N	51	51
		Std. Deviation	311.43	183.94
	medium FAI	Mean	1248.18	507.66
		N	17	17
		Std. Deviation	638.22	243.64

Tab. 20 Kondor's daily motion results

Overall, Kondor moved long distances and had long periods of activity and feeding. During lean months with low fruit availability, Kondor moved the least of the three seasons (827 m) and had a sinuosity index of 2.58. During fruit abundance, there is only one complete follow day of Kondor where she moved 2253 metres and had a sinuosity index of 2.89. Differences between the seasons were significant for the variables daily path length and nest distance (Annex 3.4).

#### Mindy

During the study period, Mindy has raised one offspring, Milo, who was estimated to have been born in the second half of 2001. Milo was weaned in 2007 but still lived in proximity of his mother. From 2004 to 2007 Mindy occupied ranges of stable size and showed little fluctuation in range size between years. On average, her annual ranges were rather small with an average of 127.63 hectares. Mindy shows a seasonal ranging pattern with significant differences between the three seasons for daily travelled path length and nest distance. Her daily travelled path length increased from the lean season when it was smallest with 744 m by almost a third to 944 metres in the abundant season. Nest distances increased in a similar manner from 351 metres to 451 meters from low to medium fruit availability and were largest in the abundant season with an average of 471 metres between consecutive night nests. Seasonal differences were statistically significant for nest distance and daily travelled distance (Annex 3.5).

Mindy	seasons		Day path length	Nest distance
	low FAI	Mean	743.59	351.35
		N	77	77
		Std. Deviation	409.53	229.56
	medium FAI	Mean	889.61	450.7343
		N	54	54
		Std. Deviation	418.39	193.41
	high FAI	Mean	944.90	471.00
		N	62	62
		Std. Deviation	365.05	191.51

Tab. 21 Mindy's daily motion results

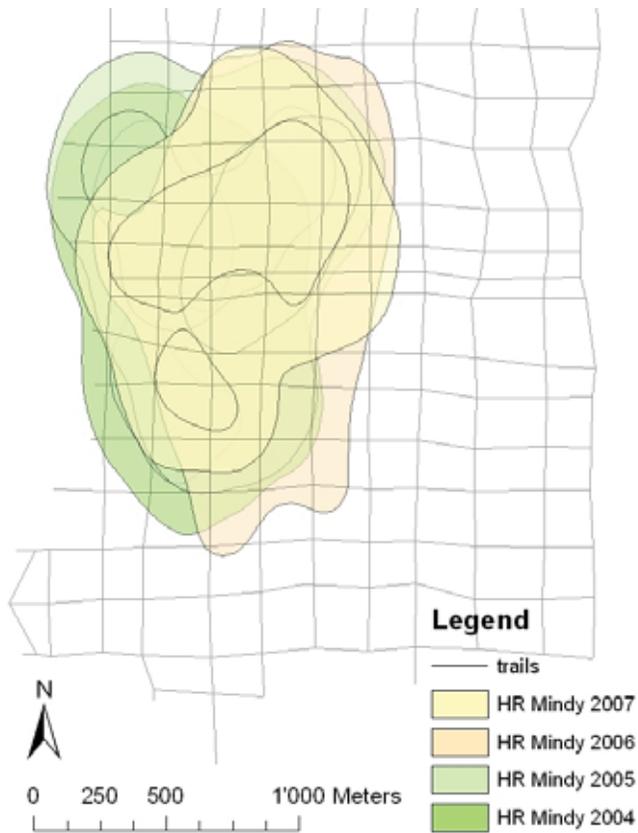


Fig. 39 Mindy's annual ranges

### Sumi

Sumi and her infant Susi moved into the study area from an adjacent area where her original habitat was presumably disturbed or destroyed. Due to constraints in sample size in 2003, her annual home range could only be estimated for 2004 and 2005 (171 ha and 166 ha respectively).

Sumi	seasons		Day path length	Nest distance
	low FAI	Mean	661.47	401.81
		N	30	30
		Std. Deviation	177.27	145.85
	medium FAI	Mean	573.42	310.96
		N	45	45
		Std. Deviation	258.42	156.59
	high FAI	Mean	738.53	359.60
		N	66	66
		Std. Deviation	326.47	194.44

Tab. 22 Sumi's daily motion results

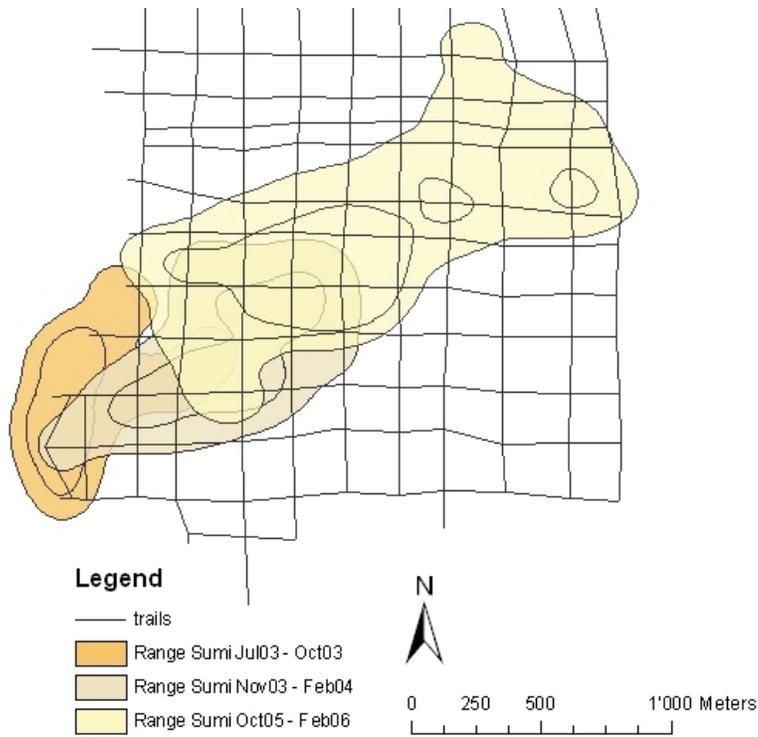


Fig. 40 Sumi gradually shifts her range

Sumi died in August 2006 by an accident or of starvation. Her infant Susi was transferred to an orangutan rehabilitation centre. During Sumi's stay in the study area it could be observed how she gradually shifted her range. Three of her seasonal ranges selected as examples show that she entered the forest from the south-west and later expanded her range and moved towards the centre of the study area (see figure 40).

During high fruit availability, Sumi had the longest travel paths (739 m), had the highest sinuosity index (2.52). Differences were statistically significant for travel paths (Annex 3.6).

Desy

Desy, one of the younger females in the forest gave birth to her infant Dery in June 2004. Desy occupied a range in the south of the study area and was less habituated than the other females described. Sufficient observations to calculate an annual home range area collected in 2007, when Desy occupied a range of 118.5 hectares. Because the year 2007 was a bad fruiting year and most months were classified as “low fruit availability”, no seasonal analysis of Desy’s individual ranging was possible.

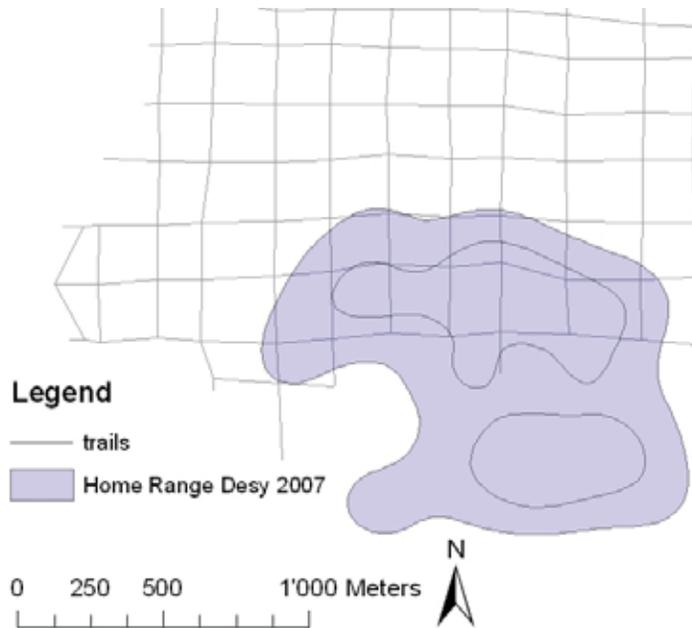


Fig. 41 Desy's home range for 2007

### 3.3.9 Relationship of movement and behavioural aspects

As seen in the previous section, individual differences in ranging behaviour were often more pronounced than seasonal influences. Therefore, the question had to be addressed whether individual differences could be entirely attributed to idiosyncrasies or whether other behavioural factors such as reproductive state, age of offspring or time spent feeding on different food items also played an important role.

#### Reproductive state

Daily travelled path length and nest distances were analysed according to reproductive state of the females, divided into two rough categories of sexually active / not active. The only two females that were sexually active during the study period were Juni and Kerry, and only they were analysed. Differences between the two females in total daily travelled paths were not significant (Mann-Whitney U,  $Z = -0.428$ ,  $p > 0.05$ ). On the other hand, differences between reproductive states were remarkable. When not sexually active, the females

travelled 703.76 metres on average ( $\pm 342.46$ ,  $n = 206$ ), whereas when they were sexually active they travelled 1124.21 metres per day ( $\pm 502.25$ ,  $n = 101$ ), which is an increase of 60% in day path length. Differences for day path length in different reproductive states were significant (Mann-Whitney U,  $Z = -7.539$ ,  $p < 0.05$ ).

Individual	Reproductive state	Mean	N	Std. Deviation
Juni	not sexually active	734.30	132	362.39
	sexually active	1268.24	31	534.64
	Total	835.85	163	450.90
Kerry	not sexually active	646.53	74	297.78
	sexually active	1060.42	70	477.19
	Total	847.73	144	445.23
Total	not sexually active	702.77	206	342.46
	sexually active	1124.21	101	502.15
	Total	841.42	307	447.56

Tab. 23 Difference in daily path length for 2 females, divided according to their reproductive state

The same pattern is repeated for nest distances, were differences between Juni and Kerry were not significant (Mann-Whitney U,  $Z = -0.488$ ,  $p > 0.05$ ), but differences between reproductive states were (Mann-Whitney U,  $z = -6.140$ ,  $p < 0.05$ ). When not sexually active, mean nest distance was 417.38 m ( $\pm 220.55$ ,  $n = 206$ ), when sexually active it was 612.49 ( $\pm 280.51$ ,  $n = 101$ ), which constitutes an increase of 46%. Orangutan females thus cover substantially larger distances when sexually active.

#### Age of offspring

For females with dependent or semi-dependent infants, day path lengths may also differ according to size and age of offspring. A graphical representation of nest distances and day path lengths in figure 42 shows the relationship of age and travel distance. In general the trend seems to be that when offspring is born, nest distances and day paths decrease until the infant reaches the age of two. Thereafter, travel distances steadily increase. The curve shows a drop when offspring is five years old. This drop is largely caused by the female Mindy that had an average day path length of 550m ( $\pm 224$ ,  $n = 54$ ) when her infant Milo was at the age of five. If Mindy's data were removed for that year, average day path length would be 976m ( $\pm 454$ ,  $n = 21$ ). With six and seven year old offspring, travelled distances increase to the former level.

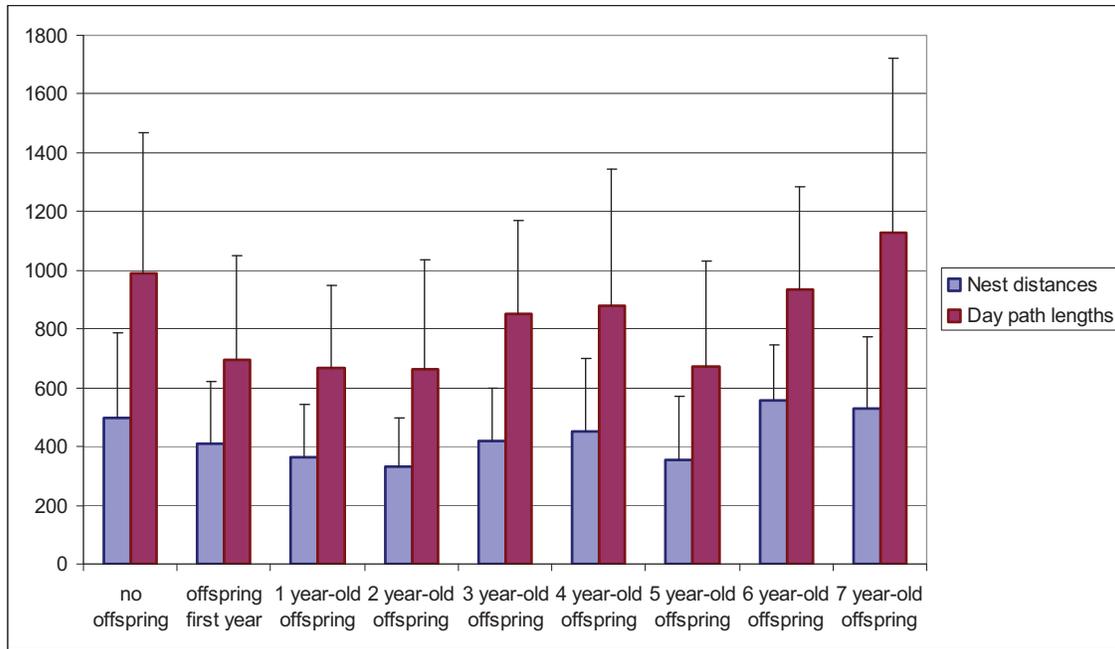


Fig. 42 Relationship of nest distances and day path lengths with age of offspring

Differences in travel distances between the different age-groups of offspring were significant (Kruskal-Wallis, Chi-Square = 106.431,  $p < 0.05$ ). As shown in table 24, percentage of the time infants clung to their mothers decreased with increasing age of infants. Up to the age of 2, infants were carried more than 80% of the time. From the age of 3 and older, infants were carried less than 40% of the time.

age of individual	Mean	Std. Dev.	N
0 - 1 year	98.35	1.76	4
1 year old	96.37	1.52	4
2 years old	84.95	7.80	3
3 years old	39.39	29.82	4
4 years old	17.78	15.64	3
5 years old	3.48	4.02	2

Tab. 24 Percentage clinging time by age of offspring

### Active Period

Female orangutans in Tuanan were on average 654.45 minutes per day active, which translates to about 11-hour-days. They were active for 656.08 minutes ( $\pm 59.35$ ,  $n = 228$ ) during low fruit availability, 649.89 minutes ( $\pm 58.88$ ,  $n = 285$ ) during medium fruit availability and 657.90 minutes ( $\pm 63.11$ ,  $n = 270$ ) during high fruit availability. Differences in total daily active period between seasons were not significant (ANOVA,  $p > 0.05$ ,  $F = 1.331$ ). Differences between individuals were significant (ANOVA,  $F = 10.503$ ,  $p < 0.05$ ). Of all females, Desy was the female who was active the longest (714 minutes, but note small sample size) followed by Mindy (685 minutes). Kerry had the shortest active periods (636 minutes).

Individual	Mean	N	Std. Deviation
Jinak	645.93	206	52.36
Juni	649.67	136	78.12
Kerry	636.59	112	61.94
Kondor	658.16	37	49.91
Mindy	685.02	150	53.54
Sumi	649.97	137	48.37
Desy	714.40	5	28.95
Total	654.45	783	60.53

Tab. 25 Daily active time of individual females

Active period correlated positively with total daily travelled distance (Spearman's rho, correlation coefficient = 0.356, sig. 2-tailed  $p < 0.05$ ) and with nest distance (Spearman's rho, correlation coefficient = 0.208, sig. 2-tailed  $p < 0.05$ ).

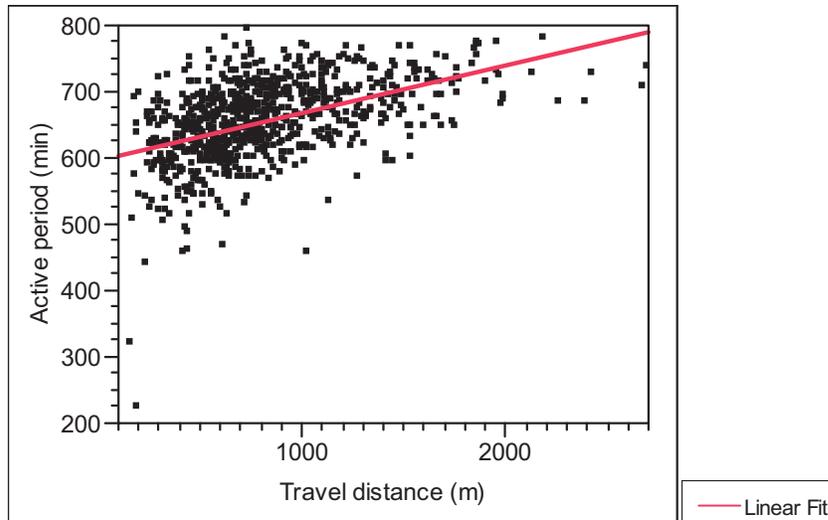


Fig. 43 Correlation of active period and travel distance

### Feeding times

Daily feeding bouts for fruit and vegetative matter were analysed for seasonality. Fruit feeding time was shortest during fruit scarcity with 267.35 minutes. During medium fruit availability it was intermediate (276.83 min) and longest during fruit abundance with 306.30 minutes. Differences in fruit feeding time were significant between the seasons (ANOVA,  $F = 8.772$ ,  $p < 0.05$ ).

seasons	Fruit feeding	N	Std. Deviation
low FAI	267.35	236	136.85
medium FAI	276.33	294	108.87
high FAI	306.30	275	86.51
Total	283.94	805	112.32

Tab. 26 Seasonality in fruit feeding

Fruit feeding correlated positively, although very weakly, with travel distance (Spearman's rho, correlation coefficient = 0.096, sig. 2-tailed  $p < 0.05$ ) and nest distance (Spearman's rho, correlation coefficient = 0.093, sig. 2-tailed  $< 0.05$ ).

On the other hand, time spent feeding on vegetative matter decreased with increasing fruit availability. During low fruit abundance, orangutans spent more time feeding on leaves (106.71 minutes  $\pm$  96.35,  $n = 241$ ) than during medium (76.22 min  $\pm$  68.87,  $n = 296$ ) or high fruit abundance (62.63 min  $\pm$  55.82,  $n = 277$ ). Differences in feeding time of vegetative matter between the seasons were significant (Kruskal-Wallis, Chi-Square 21.383,  $p < 0.05$ ).

seasons	Vegetative matter feeding	N	Std. Deviation
low FAI	106.71	241	96.35
medium FAI	76.32	295	68.96
high FAI	62.63	277	55.82
Total	80.66	813	76.45

Tab. 27 Seasonality in vegetative matter feeding time

Consequently, time spent feeding on leaves and other vegetative matter correlated negatively with fruit feeding time (Spearman's rho, correlation coefficient = -0.352, sig. 2-tailed  $< 0.05$ ). It also correlated negatively with total travel distance and nest distance (Spearman's rho, correlation coefficient = -0.242 and 0.202 respectively, both sig. 2-tailed  $p < 0.05$ ).

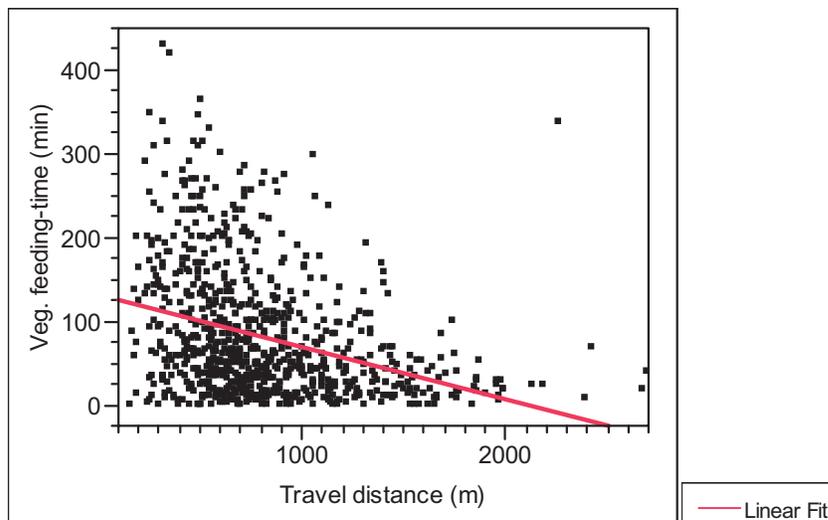


Fig. 44 Correlation of vegetative matter feeding time and daily travel distance

During fruit scarcity, orangutans spent more time feeding on leaves and less time on fruit and travel less during that time. During fruit abundance on the other hand, they fed more on fruit and also travelled farther.

### 3.3.10 Univariate Analysis of Variance –explaining variance in travel distances

The overall general linear model (GLM) model was significant (ANOVA,  $p < 0.05$ ,  $F = 31.359$ ). R Squared was 0.686 and Adjusted R Squared 0.664. Taking the large number of variables and the complexity of the model into account with the Adjusted R-Square value, 64% of the variance in the dependent variable “daily travelling distance” can be explained by the model.

Source	df	Mean Square	F	Sig.	Partial Eta Squared
Corrected Model	51	2.598	31.359	0.000	0.686
Intercept	1	18.115	218.635	0.000	0.230
Individual	6	0.198	2.384	0.027	0.019
Seasons	2	0.657	7.931	0.000	0.021
Fruit feeding time	1	1.723	20.802	0.000	0.028
Active period	1	11.385	137.407	0.000	0.158
Nest distance	1	37.303	450.228	0.000	0.381
Age of offspring	8	0.528	6.367	0.000	0.065
Individual * Age of offspring	6	0.270	3.257	0.004	0.026
Seasons * Age of offspring	14	0.218	2.633	0.001	0.048
Individual * Seasons	10	0.335	4.044	0.000	0.052

Tab. 28 Univariate Analysis of Variance for the dependent variable daily travelled distance

Except Fruit Availability Index and effect of observers (students or assistants), all factors and covariates were significant and were entered into the final model. The partial eta squared value is an indicator of the relative importance of a factor or covariate (with values between 0 and 1). Most important factors and their partial eta squared values in this model were nest distance (0.381), and active period (0.158). Also of relative importance with  $\epsilon$ -values greater than 0.05 were the covariates age of offspring. Significant interactions were found for “individual” and “seasons”, “individual” and “age of offspring”, as well as “age of offspring” and “seasons”. Although the covariate “seasons”, with the three different seasons of fruit availability was entered as significant, it was not of major importance (partial  $\epsilon$ -squared 0.021). Combining the different variables in one single model has the advantage that factors and their interactions can be represented in one model and that the effect of one variable on others is controlled for. The univariate analysis of variance has shown that several variables and their interactions have a significant effect on the dependant variable “total daily travelled distance”, of which nest distance and active period emerged most prominently.

### 3.4 Discussion

#### 3.4.1 Home range size estimates

While orangutan habitats and populations are getting smaller and smaller, it is vital to improve our understanding of orangutan space use and ranging behaviour. Whereas for Sumatran orangutans, home ranges (Singleton & van Schaik 2001) and seasonal range use patterns (Buij et al. 2002) have been studied, less is known on the seasonal space use of the Bornean species. This study aimed at providing insights into the orangutan ranging behaviour of a lowland peat swamp forest population in Central Kalimantan, Indonesia.

The question whether home ranges of Bornean female orangutans remain stable over several years can convincingly be answered in the affirmative. Females occupied the same areas during several years. Home range sizes were intermediate compared with other sites reported from Sumatra and Borneo (Singleton et al. in press: 206). The results from this study fit well with reported variation in orangutan subspecies with *Pongo pygmaeus morio* having smallest ranges, *Pongo pygmaeus wurmbii* (both in Borneo) having intermediate ranges compared to *Pongo abelii* (in Sumatra) having largest.

For example in Sumatra at the Suaq Balimbing study site, Singleton & van Schaik (2001: 877) reported estimated female home range sizes of 850 hectares with polygon methods. Compared with Suaq, mean home range in Tuanan was 280 hectares (range 172 – 379 ha, also estimated with polygon method, but note difference in study duration).

Study site	Subspecies	Habitat	Study duration in months	Home range ha
Kinabatangan	<i>P. p. morio</i>	homogeneous	48	180
Mentoko	<i>P. p. morio</i>	homogeneous	18	> 150
Tuanan	<i>P. p. wurmbii</i>	homogeneous	24	170 - 380
Gunung Palung	<i>P. p. wurmbii</i>	heterogeneous	103	600
Ketambe	<i>P. abelii</i>	homogeneous	48	300 - 400
Suaq Balimbing	<i>P. abelii</i>	heterogeneous	52	> 850

Tab. 29 Home range sizes calculated with polygon methods grouped by island subspecies (all values except Tuanan based on Singleton et al. in press: 206).

Home range sizes seem to be considerably smaller in Tuanan than they are in Suaq. This can be attributed to different factors. First, it was argued that the low species richness of the Suaq swamp results in a clumped distribution of fruiting tree species, leading orangutans to use a larger area to maintain an adequate diet (Singleton & van Schaik 2001), e.g. the orangutan diet at Suaq contains 61 plant species, whereas the swamp forest in Tuanan contains around 125 species (van Schaik & Singleton, unpublished data). Second, as has been shown in the first part of this thesis, methodological aspects may be of importance. Home range estimates in previous studies were largely based on the use of grid-cell-count methods or polygons whereas this study reported seasonal ranges based on kernel estimates. Comparisons are thus rather qualitative than quantitative and should be

interpreted with caution. To facilitate comparisons with previous studies, MCP estimates were also included for home ranges. However, this practice can only be seen a dissatisfying resort and should be discontinued as more and more studies will hopefully start reporting ranges based on kernel estimates.

Knott et al. (2008) reported home ranges from Gunung Palung, Borneo with different grid-cell methods and minimum convex polygons. Polygons based on 100% of locations gave estimates of 595 ha for Gunung Palung. For Tuanan, polygons based on 95% of points gave estimates of 280 hectares. Differences in mean home range size between Gunung Palung and Tuanan can only to some extent be attributed to the difference in percentage of locations selected. Estimates based on all points are likely to include outliers (i.e. 'excursions') and overestimate home ranges. Although there are a series of methodological issues involved when comparing range estimates from different sites, differences between study sites and the two islands of Borneo and Sumatra seem to be real. Thirdly, differences between the reported means may be attributed to differences in habitat quality and population density between the sites. For some sites, much larger home ranges are reported, even if they harbour the same subspecies. For example Gunung Palung has larger range estimates than Tuanan and Sabangau (all *P. p. wurmbii*) (Singleton et al. in press: 206). The most likely explanation for this variation is the nature of the habitat mosaic. Whereas habitats are rather homogeneous in Tuanan and Sabangau, the habitat mosaic is more heterogeneous both in Gunung Palung and Suaq Balimbing. The Suaq and Gunung Palung sites both contain several distinct habitat types, i.e. swamp and dryland forests in a mosaic scale that can be traversed by individuals with one or two day's travel (Singleton et al. in press: 207). It has also been suggested that Sumatran forests, due to their soils with volcanic origins are more productive than Bornean forests (van Schaik 1999), a notion that is supported that in similar habitats, orangutan density is higher on Sumatra than on Borneo (Delgado & van Schaik 2000: 208).

In summary, orangutan home ranges seem to be species-specific. Furthermore, differences in home range sizes can be attributed to factors such as fruit species-richness of the habitat and nature of the heterogeneity of the habitat mosaic. As this study showed that there are several issues involved when analysing ranges, attention has to be paid when comparing ranges estimated with different methods. This will assure that differences between studies and sites are meaningful and not based on methodological differences.

### **3.4.2 Seasonal and individual variation in range size**

Availability of preferred food items varies within and between years in Southeast Asian forests (Knott 1998: 1062), and thus in Tuanan. Environmental seasonality was hypothesised to influence feeding and ranging behaviour of orangutans in Tuanan and the research

question was addressed whether female orangutans change their ranging behaviour during times of food scarcity or abundance.

In order to analyse inter-annual seasonal variations, the year was divided into different fruiting seasons using fruit availability data from two phenological plots. Availability of edible fruit strongly correlated with overall fruit availability and the latter was used to define fruiting seasons. This practice was also adopted in previous studies and was not found to influence results (Wich et al. 2006: 342).

If analysed at the seasonal scale, ranges and core areas were larger when fruit was scarce, but differences were small and not statistically significant. This indicates that orangutan females do not change the size of their ranges according to fluctuations in fruit availability. Seasonal range and core area overlaps were used to assess the possibility of interactions between females. With increasing core area overlap, the probability of encountering neighbouring females also increases. Core area overlaps were slightly larger in the lean season, but the difference was not statistically significant. No seasonal effect was found, either in overlap of seasonal ranges or in core area overlaps. According to these findings, the postulated hypothesis that orangutans expand their ranges and have higher overlapping areas when fruit is abundant has to be rejected. The question whether the spatial tolerance between individuals differs depending on food abundance can be answered in the negative. Orangutan females did not retreat into distinct (non-overlapping) core areas when fruit became scarce. Results from the analysis of seasonal ranges did not reveal any significant influences of fruiting seasonality on range sizes and spatial tolerance among females.

As orangutan females do not seem to be range-shifters in Tuanan, this confirms the postulated hypothesis that shifting into a different range is not profitable in the rather homogenous peat swamp forest. Rather, costs of moving into an unknown area seem to outweigh the possible gains of accessing new food patches. These results suggest that ranging behaviour differs markedly between habitats. Whereas Sumatran orangutans in hilly terrain exhibit strong seasonal ranging patterns when they follow fruiting peaks along altitudinal bands (Buij et al. 2002: 83), Bornean orangutans living in a peat swamp forest were not found to react to seasonality in terms of range size or range shifts.

There seems to be considerable variation in home range sizes between individuals from the same study site. Some of this variation is explained by reproductive state: females tend to cover larger areas during their mating period. Apart from the variation in home ranges that can be explained by the reproductive state, certain variation in home range sizes between individuals remains that is not attributable to the aforementioned factor. Differences might be due to differences in habitat quality or productivity between individual home ranges, but it was argued that the peat swamp forest in Tuanan consists of a homogenous habitat.

However, variation might be found at small-scales and individuals able to secure access to comparatively more productive patches would obtain a competitive advantage. Only females with a relatively high position in the dominance hierarchy would be able to gain and maintain access to such patches. This would fit with data from Tuanan, where Mindy and Jinak (dominant females) have the smallest home ranges. As dominant females they can range wherever they want, making the subordinate females leave. Thus, the ranges of subordinate females will be larger on average because they, too, will try to stay in the more productive patches whenever they can.

### **3.4.3 Utility of home range estimations with kernel methods**

Having seen the large variability that is caused by the different factors in home range estimations (chapter 2.5.6), another explanation for the persistent range sizes might be that home range models such as kernels are not appropriate methods for depicting and analysing differential movement patterns in orangutans. The home range concept may be adequate for determining ranges at large temporal scales such as years. Due to the large variability of the ranging estimator, smaller temporal scales are difficult to analyse as the variance of the model blurs any underlying spatio-temporal pattern, if present. Many organisms, including mammals, have been shown to change their habitat use according to seasons. In extreme cases, some wildlife species, such as grey seals (*Halichoerus grypus*) and polar bears (*Ursus maritimus*) researched by Harvey et al. (2008) and Ferguson et al. (1999), respectively were shown to use seasonally distinct home ranges. Those conclusions were successfully drawn with kernel home range estimation methods. However, with wildlife such as polar bears that exhibits a strong seasonal migration pattern the spatial scale of range changes is completely different. If Bornean orangutans in Tuanan show changes in their ranging behaviour for the fruiting seasons at all, these changes are too small to be represented with kernel range estimations. For finer temporal granularities such as seasons, other spatial indicators than range should be applied.

Another issue for estimating home ranges of arboreal mammals has been brought up by Rader (2006: 577) as depicting the range of tree-dwelling animals in two-dimensions can be a serious under-estimation of their actual range. Rader therefore suggest the use of a three-dimensional range to account for the different dimensions of vertical and horizontal space use in tree-dwelling animals. This suggestion can be extended to animals moving in fluid media or air, such as marine mammals and birds. For example, Harvey et al. (2008) successfully modelled seasonal space use of grey seals in three dimensions. Modelling orangutan home ranges in three dimensions may shed light on the vertical dimension of space use and thus help to capture ranging responses to environmental factors in more detail.

As orangutan females are essentially non-territorial (van Schaik et al. 2005: 249) and are also not central-place foragers, the utility of estimating “home ranges” is debatable. Terms such as “annual” or “seasonal” range with an explicit temporal component might be more useful concepts for orangutans and other non-territorial animals. Furthermore, applying kernel methods for range estimations involves the risk of producing range data that are not comparable with other studies, as was clearly demonstrated in this study. The difficulty in comparing results from different studies has led to the co-existence of several models and to the persistence of the MCP model in range studies (see for example Hötzel et al. 2007 and their study on European wild cats *Felis silvestris*), which is often included as a second reference model. However, because the MCP method is known to include possibly large, unused areas, researchers have resolved to remove such “unused” areas where no observations were made from the overall area estimate. Defining unused areas is not only a highly subjective procedure, it also depends on the sample size and results are thus difficult to reproduce and compare.

The lack of consensus in wildlife biology on what models to apply, even for a single species, is highly unsatisfying. What future do home range estimation models, especially the kernel method, have? This will largely depend on whether the difficulties in comparing studies from different researchers and sites can somehow be overcome.

#### **3.4.4 Representing travel paths with geospatial lifelines**

An example of a method with less associated uncertainties is the analysis of so-called “geospatial lifelines”. Lifelines are the spatio-temporal representations of trajectory data from moving point objects. The method has been applied to a variety of other fields such as devising optimal cattle grazing strategies in livestock management and human movement analysis in sports games (Laube et al. 2007: 483). The advantage of geospatial lifelines is that the temporal and spatial resolution of the lifeline can be varied. For every discrete point in space, movement descriptors such as speed, acceleration and direction can be applied. Different temporal windows allow the analysis of movement derivatives such as sinuosity over varying time frames and at different points of the lifeline (Laube et al. 2007). Geospatial lifelines constitute an ideal tool also for analysing wildlife movement data because results are based on observed locations and no estimates have to be made.

In this study, the geospatial lifeline concept was applied to orangutans, whose locations were usually recorded every half hour. The geospatial lifeline composed of the different observed locations is a generalized depiction of the animal's real travel path. Therefore, the problem of line generalization very well known in cartographical sciences also applies to generalized orangutan paths. Namely, the more the line is generalized, the shorter the line will be. Longley et al. (2005: 105) illustrated this problem using the coastline of Maine: if a

defined segment of the coastline was measured using 100 kilometre intervals between measurements, its length would be approximated with 340 kilometres. If the divider span was halved to 50 kilometres, the approximated line length would increase to 355 kilometres, with 25 kilometres spans it would still further increase to 415 kilometres and so on. Theoretically, with ever shorter divider spans, the length of the coastline would stretch towards infinity and is indeterminable. Any approximation of a line is therefore scale-dependent. It can thus be argued that comparisons for travel routes of different individuals across seasons are valid, because the same amount of generalization applies to all the data and they are thus all represented at the same scale. In addition, as we have already seen, range use of arboreal mammals is essentially three-dimensional and line lengths only represent the horizontal dimension of travel paths. Deriving energy budgets from the estimated travel distances is therefore discouraged.

### 3.4.5 Variation in travel distances between sites

Daily travel lengths reported in this study fit well with reports from other sites. If possible, only values for mothers with dependant infants were included as differences in travel distances reported in this study differed significantly between reproductive states. Table 30 shows that daily travel distances are smallest for *P. p. morio*, whereas those of *P. p. wurmbii* and *P. abelii* are approximately similar. Females at ecologically more heterogeneous sites (e.g. Gunung Palung and Suaq) do not seem to have distinct day journey lengths to those at more homogeneous sites (Tuanan, Ketambe). Thus, females living in heterogeneous habitats do not need to increase their mean daily path lengths to switch between habitat patches, as these journeys can usually be made with journeys that lie in the range of the normal day journey lengths (Singleton et al. in press: 210).

Study site	Subspecies	Habitat	Daily path lengths in meters	Mothers / all
Kinabatangan	<i>P. p. morio</i>	homogeneous	162	all
Mentoko	<i>P.p. morio</i>	homogeneous	305	all
Tuanan	<i>P.p. wurmbii</i>	homogeneous	713 ( $\pm$ 353)	mothers
Gunung Palung	<i>P.p. wurmbii</i>	heterogeneous	690	all
Ketambe	<i>P. abelii</i>	homogeneous	675 ( $\pm$ 282)	mothers
Suaq Balimbing	<i>P. abelii</i>	heterogeneous	833 ( $\pm$ 306)	mothers

Tab. 30 Daily travel path lengths for different study sites and island subspecies (Tuanan: this study, other values from Singleton et al. in press: 210).

### 3.4.6 Seasonal variation in daily travel distances

If only annual average daily travel distances are reported, much of the underlying variation e.g. due to seasonality is destroyed. Significant differences in daily travel distance and nest distance were found for the three fruiting seasons (low, medium and high fruit abundance). Using a different approach to analyse ranging, the question whether female orangutans

change their ranging behaviour according to fruit availability was answered in the affirmative. With little fruit available, orangutan females travelled less and had smaller nest-to-nest distances. When fruit was abundant travel distances as well as nest-to-nest distances increased. Nest and daily travelled distances correlated weakly with the fruit availability index, also indicating that they increase as available fruit increase. In her study, Haag (2007: 84) found no correlations between travel distance and edible fruit availability index and also no significant differences in daily distance travelled between times of food abundance and scarcity. This is likely to be due to smaller sample sizes ( $n = 38$ , this study  $n = 971$ ) rather than due to the use of the edible fruit availability index. Previous studies also indicated that the choice of overall fruit availability does not influence results (Wich et al. 2006: 342). However, using the concept of fruit availability has also been criticised, as it is based on the assumption that fruit availability mirrors what is available for orangutans. This may not be realistic, as overall fruit availability does not take the nutrient content of fruit into account (Knott 2005: 354). In an orangutan population in West Kalimantan Knott (1998: 1077) found that caloric intake varied markedly between intra-annual seasons. Caloric intake was higher during mast-fruiting events than would have been expected by fruit availability alone, as mast fruiting species seemed to have higher energy contents than non-mast species (Knott 1998: 1069). As the peat swamp forest in Tuanan is not subject to mast fruiting events it can be argued that the comparing fruit availability and feeding times yields reasonable estimates of overall food availability and consumption. However, the fruit availability index does not necessarily accurately reflect the actual amount of fruit available. There may still be variation between years in crop size that influence actual food availability for orangutans (pers. comm. M. van Noordwijk) and future studies might take this into account to depict more exactly what is available for consumers.

Nest distances were strongly correlated with daily travelled distances. This is also the reason why the sinuosity index did not show any seasonal effects. Being an index it shows the relationship of length of nest distance to total daily travelled path. If both measures decrease at similar rates there is no visible effect in sinuosity, as was found. The ratio of nest to travel distances remained around 2. Orangutan females thus moved twice as far as they build their nests apart, irrespective of seasons. In general, when there is more fruit available, orangutans travel more than when little fruit is available, but the large-scale movement pattern represented by the sinuosity index does not differ seasonally, indicating that orangutans do not change their large-scale search patterns.

### **3.4.7 Individual variation in ranging behaviour**

A seasonal influence on ranging behaviour of female orangutans was found, but also differences between individuals. To explain the variance between individuals, more aspects were taken into account, such as the reproductive state of the female and age of infants, if present. During their mating period, the females travelled 60 percent more than when they were not seeking the association with males. Furthermore, the effect of age of infants on travel distances was analysed. After having given birth, orangutan mothers' path lengths dropped and remained small during the first three years of an infant's life (until the age of two). Afterwards, females with infants almost steadily increased their travelling distances until they reached their former level when the offspring was about six years old. This pattern is probably best explained by the energy-costs for lactating females of carrying infants clinging to them. At the age of two to three, although heavier than after birth and drinking more milk as they get larger until the point that their own food intake begins to make a significant contribution, infant orangutans can already travel some distance on their own, and would thereby reduce energy-costs for their mothers of carrying them. This was shown for Sumatran orangutans: until infants are 2 years of age, they are carried by the mother more than 80% of the time she travels. Offspring of 3 years or older are carried by their mother less than 20% of her travel time (van Noordwijk & van Schaik 2005: 82). In Tuanan, infants younger than 2 clung more than 80% and from 3 years on, they clung less than 40%. The weight of clinging infants thus seems to influence travel distances, as it was shown that with decreasing amounts of clinging, mothers increased travel distances.

### **3.4.8 Seasonality in feeding behaviour**

Seasonal changes in the environment may not only produce ranging responses in orangutans, but also behavioural responses that interact with one and another. In order to complement the analysis of ranging seasonality, differences in length of fruit feeding bouts and feeding bouts of leaves and other vegetative matter such as twigs and bark were analysed with regard to the effect of fruiting seasons. When fruit was scarce, orangutans spent significantly more time feeding on vegetative matter than when fruit was abundant. The pattern for fruit feeding was exactly the opposite: frugivorous orangutans spend increasingly more time feeding on fruit with increasing abundance of their preferred food items. This results show that orangutans are probably using periods of high fruit availability to build up energy stores, rather than trying to achieve a constant net food intake at all times, which supports the findings of Knott (1998: 1075). Knott showed that when fruit is abundant orangutans are able to take advantage of this period to put on additional fat stores by feeding on energy-rich fruit.

The results from the ranging and behavioural data of this study further support the hypothesis that orangutans pursue an energy-intake-maximizing strategy in times of high fruit abundance: they were shown to travel longer and consume more energy-rich fruit and reduce feeding time on low-energy foods. In the lean season they switch to an energy-expenditure-minimizing strategy: females feed on “what’s there” and easy to reach, thereby reducing energy-costs for foraging, which is reflected in reduced travel distances. The findings of this study are also in accordance with Knott’s results that during the period of low fruit availability orangutans, especially females, are not able to maintain their body weight (1998: 1075) and are expected to reduce travel and thus energy expenditure. Taking feeding times and behavioural states into account thus gave a more complete picture of orangutan ranging responses to fruit scarcity in Tuanan.

#### **3.4.9 Issues for Conservation**

The main issues for conservation that arise from this thesis are as follows: This study has shown that orangutans in different states of their life histories have differential spatial needs. Actual space needs can be two to three times as high during certain periods than average ranges. Furthermore, results suggest that environmental seasonality does have an effect on orangutan activity and range use, without, however, affecting range sizes. Apart from the influence of climate change, human impact on the environment is likely to further increase seasonal effects and reduce habitat quality. Those changes will also negatively affect orangutan populations and it is therefore vital that we further improve our knowledge of orangutan ranging behaviour. Individual space use can be a critical determinant of survival and, ultimately, reproductive success in a species (Murray et al. 2008: 23). This study provides an example of how behavioural research and spatial analysis of individual movement patterns can help to produce important information that may enhance the persistence and management of a species at risk.

#### **3.4.10 Travel and Cognition**

The presented findings offer some explanations why orangutans range the way they do. However, many of the underlying processes that lead to the observed ranging patterns still remain to be investigated. Several questions concerning spatial strategies of orangutans are yet to be answered. For example: Are foraging paths chosen by orangutans efficient routes? What are the best search strategies to discover unknown resources in the forest? How do orangutans decide where and when to forage?

There seems to be a universal tendency in the animal kingdom to reduce travel time and effort. However, it is not at all apparent how this is achieved (Janson 2000: 165). Different models to explain spatial foraging have been devised which incorporate varying degrees of

spatial memory. The simplest models assume that no spatial memory of resources exists. If an animal does not know where to find the next patch of resources, and if resources are depletable, the best it can do is to move in a straight line. Any turns are likely to bring the animal back to areas that it has already searched (Cody 1971). This fact led Janson (2000: 173-174) to ask for caution when interpreting animal movement patterns: “*Although animals moving between two known resources should clearly prefer to go in a straight line, the use of straight-line movement is not by itself convincing evidence of goal-oriented movement*”. Even the contrary has been observed: that goal-oriented movement need not be reflected in straight lines. Noser and Byrne (2007: 263) showed that route linearity and travel speed were not always associated with goal-directed travel in wild chacma baboons (*Papio ursinus*). On the other hand, if animals locally deplete resources but cannot remember exactly when they exploited them, their best long-term strategy is to delay their return to that place for as long as possible. Without spatial memory, the only way they can delay returning to previously exploited areas is to move directly away from them, a goal which is achieved by always moving in a straight line. Although most foragers will be forced by spatial constraints in the form of home ranges or territories to return toward previously used areas, moving in straight lines will generally maximize return times to a given location (Pyke 1983). Several studies have evaluated to what extent foragers move in straight lines, a strategy that is predicted when resources are renewed slowly, are not patchy and spatial memory is absent or poor (Janson 2000: 187). A tendency to maintain such a consistent foraging direction was for example shown for individual bumblebees (*Bombus* sp.) when foraging on moderately clumped flower patches (Stolz 1986: 19).

Things become considerably more complex when foragers have mental representations of and are able to remember the distribution of food sources. The problem of optimal foraging with spatial memory has also been formulated in different contexts in other areas of research. The classic problem in economic geography is known as the “travelling salesman problem”, in which a salesman needs to find the shortest route through  $n$  stops. The salesman has to begin and end at the same location but must not revisit any other stop. Essentially, foragers are also “salesmen”, needing to visit a set of given food patches in an optimal order. The aforementioned problems belong to a group of difficult mathematical problems termed Nondeterministic-Polynomial (NP)-complete problems. NP-complete problems are difficult to solve because all known algorithms for the *guaranteed* best solution require computation times that increase exponentially with the number of points to be visited. Despite decades of work, mathematicians have not found a solution to this problem that increases only as a polynomial function of  $n$  (Janson 2000: 171-176). Finding the best possible solution is extremely difficult for most animals and humans without computers. Therefore, it seems unlikely that animals in the wild determine their travel paths in a

travelling-salesman-like manner. Rather, they are assumed to use rules of thumb that provide rough guesses of the optimal solution. Such rules of thumb imply mechanisms that are more realistic to be used by animal or human brains (Janson 2000: 175 - 177), and reach solutions very close to the optimum.

Formulating different hypotheses of foraging strategies is one thing, providing evidence from wild animals another: “*Obtaining convincing evidence of spatial memory from unmanipulated wild animals is difficult, to put it mildly*” (Janson 2000: 188). Testing for the existence of mental maps in animals is further complicated by the difficulty to formulate a null hypothesis. There is no universal null model of random foraging in two dimensions. Realistic models need to incorporate species-specific parameters such as known or assumed movement distances and turning angles and distances at which food can be detected. In order to compare results of such simulations, researchers must know essentially everything about the set of resources that could be discovered by the animals, also about resources that have not been used previously. Those requirements can rarely be met in the wild. On the other hand, captive experiments can clearly control what the animal can detect and what new resources are available to be detected. However, the skills involved in foraging across restricted spaces with a lot of available landmarks may be quite different from those needed for large-scale foraging across entire landscapes. It is not clear whether captive-born animals can ever develop the ability to navigate across landscapes, even if their wild-born relatives are able to do so. None the less, there is strong experimental evidence across species that many foragers have spatial memory of their foraging sites and that this knowledge increases their foraging success (Gallistel 1990). Experiments conducted on primates have demonstrated the presence of spatial memory and representation abilities, for example with a captive Bonobo (*Pan paniscus*) that was able to navigate in a goal-oriented manner and use previously unknown short-cuts to get to his destination within a 20 hectares wood (Menzel, Savage-Rumbaugh et al. 2002: 601). For wild chimpanzees (*Pan troglodytes*), Boesch & Boesch (1984: 160) concluded that their study animals in the Tai National Park possessed spatial memory and were also able to somehow measure distances, which indicates the existence of Euclidian mental representations of space.

Considering reports of spatial memory from related great ape species and the anecdotic evidence from the field (e.g. MacKinnon 1974) that orangutans “arrive at the right place at the right time” it is likely that orangutans also possess mental representations of space and are somehow able to remember the locations of fruiting trees in their range. However, to demonstrate that orangutans possess spatial memory abilities in the wild is, even with clever experiments, almost impossible without leaving many other alternative interpretations.

### 3.4.11 Evolution of optimal cost-benefit travel routes

Far fewer studies investigated how efficient the spatial foraging decisions were or what the best behaviour *would* be. As animals have limited time and energy available for foraging, natural selection should have favoured individuals that maximized benefits from foraging relative to costs. Minimizing travel distances is perhaps the most obvious strategy that contributes to an optimal cost-benefit balance. It was suggested that over evolutionary timescales, there should have been a strong selection pressure on the ability to remember 'what' can be found 'where', and to find the corresponding location by the shortest possible route (Noser & Byrne 2007: 257). If the need to forage efficiently has selected in primates for an ability to "think ahead", why are frugivorous primates smarter than their relatives who subsist on leaves or insects? This contrast persists, even if the important effects of group size on relative brain size are accounted for (Barton 2000: 219-220). The patchy distribution and ephemeral nature of fruit sources has led researchers to argue that large brains are needed to memorize and integrate information on the location of such resources in space and time (Barton 2000: 205). However, it can be argued that the distribution of leaves can also be patchy and ephemeral, especially for young leaves (Glander 1982). Furthermore, the cost of terrestrial locomotion is three to four times greater than for flying animals (Schmidt-Nielsen 1972: 225) and will be even higher for arboreal animals that have to climb up and down trees. Fruit-eating bats might therefore be a lot less concerned about the efficiency of their flying-routes than orangutans. As arboreal quadrupeds, orangutans face much higher costs of longer foraging routes than flying animals and might have been submitted to stronger selection for optimal cost-benefit travel routes. Following this train of thought, travel routes of orangutans should have been optimized and would at best be adapted to the prevailing food availability.

This study provides evidence that orangutans show seasonally dependent foraging and ranging behaviour. When fruit is abundant, they forage more on fruit, reduce feeding times on vegetative matter and travel longer distances between fruit trees. However, the current results do not allow conclusions to be drawn about the efficiency of these foraging paths. Future work should aim at describing orangutan movement patterns in more detail. Attention should be paid to smaller temporal scales to explore spatial foraging and movement strategies in order to address questions regarding the challenges (i.e. the ability to integrate spatial, temporal and ecological information) orangutans face in locating and exploiting food resources in a changing environment. However, the difficulty for this research will be to formulate quantifiable and testable hypotheses.

## 4. General conclusion

### 4.1 Achievements

In this study, the underlying uncertainties in spatial orangutan data were investigated by comparing two different field methods. It was shown that neither manual mapping nor GPS data collection introduced large errors into spatial data. Other uncertainties in home range models were analysed by comparing effects of parameter selection and sample sizes on model results. A significant effect of the home range model on range sizes was found, which indicates that comparisons between models are further complicated by the use of different models. Regardless of the home range estimation method used, differences between individuals were significant. Although autocorrelation was present in the data, it was not found to significantly influence orangutan range estimates. On the basis of these methodological analyses a procedure to calculate home ranges was arrived at which is objective, reproducible and based on real movement data. Consequently important lessons were learned for future range studies in orangutans and other species. Furthermore it was ensured that the ranging analyses are meaningful and not based on methodological errors.

A key point of this study was to apply these spatio-temporal models to analyse the seasonal movements of orangutans. Orangutans primarily feed on fruit when it is abundant. Therefore, seasons were divided according to fruit availability. As was shown by comparing seasonal ranges, ranges remained stable irrespective of fruit abundance. Apart from comparing ranges across seasons, another method was applied to analyse space use at a different temporal scale: daily travelling distances and distance between consecutive night-nests were measured to analyse whether seasonal movement patterns were present. A marked difference was found between seasons of high and low fruit abundance: When fruit was scarce, orangutans foraged more on vegetative matter and travelled shorter distances. On the other hand when fruit was abundant, they significantly increased travel distances. Orangutan females thus do show seasonal changes in their feeding and ranging behaviour. However, those responses are not reflected in range size, but in the manner *how* the range is used.

### 4.2 Implications

The comparison of results from different home range models, parameters and sample sizes showed that all factors had an influence on range estimates and introduce uncertainties into model estimates. However, differences between individuals were consistent regardless of sample size. This indicates that comparisons between studies are possible, but only if prerequisites for comparative studies are met, e.g. that similar models and methods are used. For the aforementioned reasons, comparisons across studies that use different space

use models should be treated carefully. The methodical part of this study made it clear that there are a lot of issues and uncertainties involved when applying home range models to analyse animal space use. However, most of these matters can be resolved by conducting preliminary analyses and using objective methods for model and parameter selection. Moreover, apart from thoroughly reporting methods applied to model ranges, efforts should be put into designing guidelines for researchers that enable meaningful comparisons between studies. As these guidelines should at best be biologically informed (e.g. animal's mobility, tendency for home ranges to shift, tendency to move out of regular range when in estrus) to such an extent that complete comparability among studies may be difficult or impossible to achieve. Furthermore, home range models are applied to a great variety of species that not only differ in terms of the medium where they primarily move (air, water or land), but also in appearance and behaviour. Finding a home range model and sample size that fits all these different features well and is in accordance with each studies' objectives is neither possible nor desirable. Rather, it should be attempted that researchers studying the same species agree on methods used so that comparisons across studies will be possible. Otherwise, studies aiming at comparing animal space use between sites or subsequent studies may face serious obstacles. Such comparative studies will become ever more important as biologists and ecologists strive to detect and anticipate impacts of climate change on different habitats and organisms living therein.

Although there was no seasonal effect of range size, the findings of the analysis of travelling distances support the postulated hypothesis that in times of relative food abundance, orangutans pursue an energy-intake-maximizing strategy. They travel more, visiting different trees when they bear fruit or flowers, which results in larger travel and nest distances. When fruit availability is high, female orangutans eat less vegetative matter because they have better, energy-rich food available. In times of fruit scarcity on the other hand, instead of fruit they feed more on relatively low-energy foods such as leaves, twigs and bark that are less spatially dispersed and can therefore be exploited by spending comparatively less energy-cost on travelling than needed to feed on fruit.

Some primates tend to have rather broad reaction norms which allow them to react to and cope with seasonality up to a certain point. However, if these reaction norms are exceeded or the climatic change is too fast, species are at a high risk of extinction (van Schaik & Brockman 2005: 16). Analysing responses of orangutans to past and recent seasonality can thus be used as a baseline to appraise effects of climate change in the near future.

### **4.3 Future work**

This study further supports the hypothesis that there are significant differences in space needs between orangutan species living in different habitats on the islands of Sumatra and Borneo, respectively. Although a seasonal impact on orangutan ranging patterns was found for Bornean orangutans, relatively little is known about the differential ranging patterns of the two species. This study provides an example of integrating both spatial and behavioural data to analyse responses to seasonality. A more detailed analysis of behavioural data than presented in this study may be able to answer the question why orangutans move the way they do. Furthermore, spatial foraging patterns of orangutans have not been investigated in detail and little is known to what degree foraging paths are optimized as compared to other frugivorous primate species.

As male orangutans have much larger ranges than females and are difficult to follow, little is known about their movements. A question so far unaddressed by quantitative studies is how flanged and unflanged males differ in their ranging behaviour. Future research should thus aim at filling this gap in the knowledge by integrating behavioural and movement analyses.

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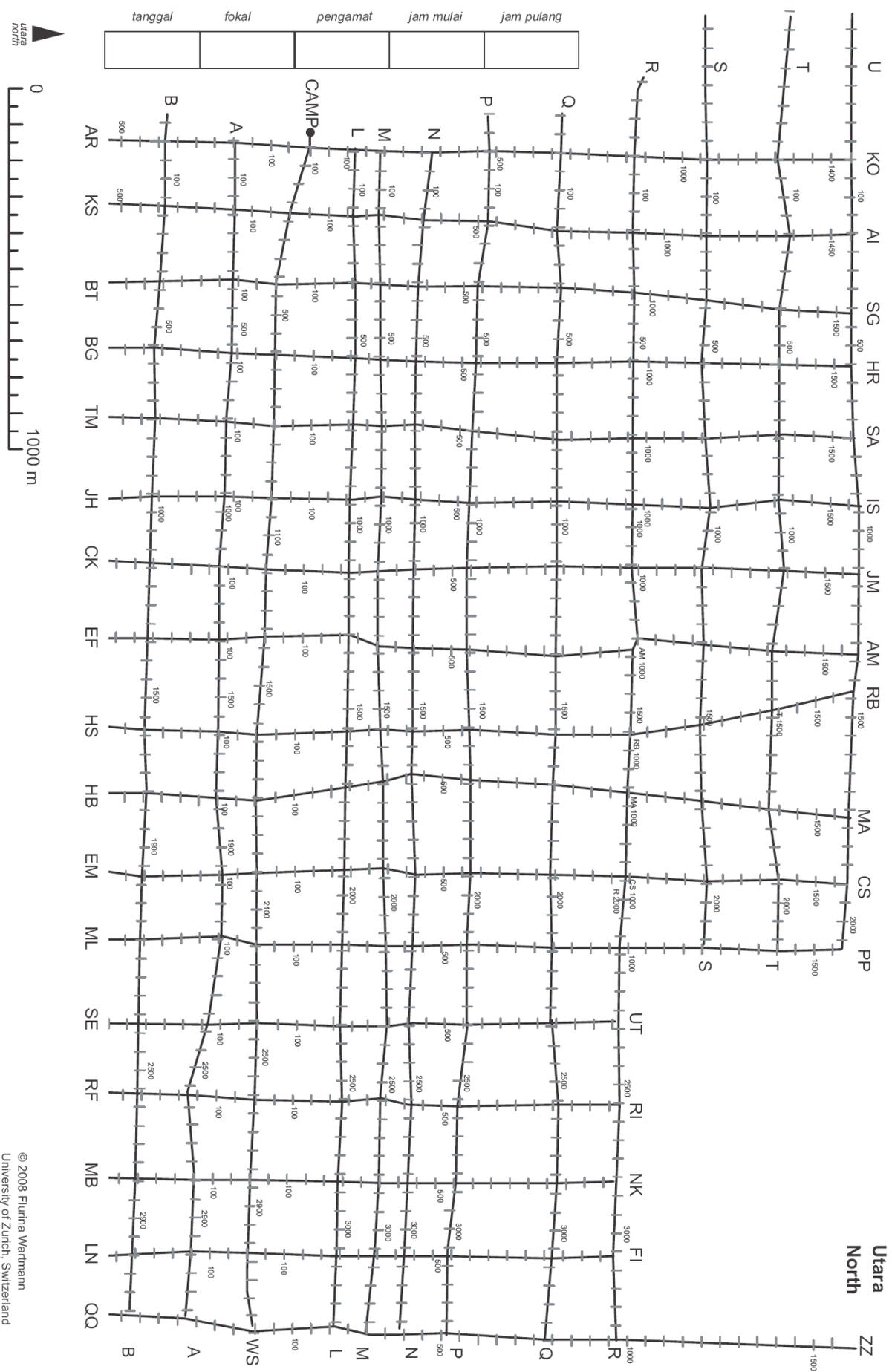
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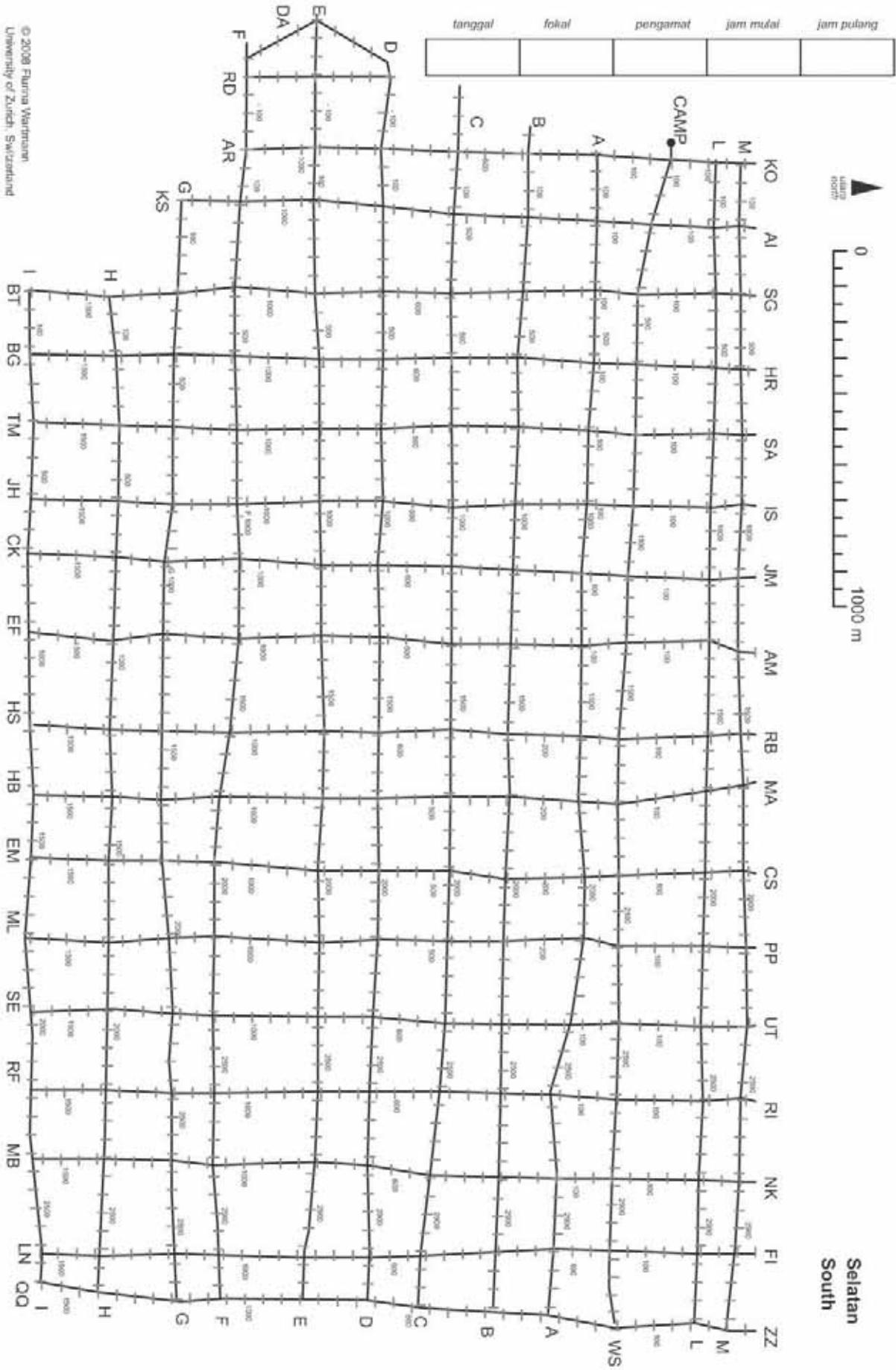
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Annex 1.1



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Annex 1.2

## Annex 2 Guidelines for field data collection with GPS

### *Introduction:*

The Global Positioning System (GPS) is a satellite-based navigation system. 24 satellites are moving around the earth at a height of 20'000 kilometres. The satellites are constantly transmitting radio signals that can be received by anyone with a GPS. The GPS receiver uses the radio signals to calculate the distance from the satellite and determines where the user holding the GPS is located.

With a minimum of three or more satellites, the GPS receiver can determine a position in East/South coordinates (latitude/longitude). With four or more satellites it can also determine altitude above sea level. By continuously updating your position, a GPS receiver can also provide data on your speed and direction of travel (WHO 2003).

### *Settings:*

There are many different GPS devices from different brands. For information on how to change the settings on your GPS have a look at the GPS user guide that came with your device. Make sure the settings on your GPS are correct before starting with data collection. There are several different GPS location formats. You should check that everybody who is working on the same project is also using the same format and same reference grids.

- The reference ellipsoid defines the geographic coordinate system of your location data. Select WGS 1984 (World Geodetic System).
- Units of your position should be the same for all GPS data. A good format that can also be easily converted is geographic coordinates (latitude/longitude) in decimal degrees. For example: E 114.44095, S2.151616 is a position in decimal degrees.

If your coordinates look like this: E 114° 26.457', S 2° 9.097' or like this: E 114° 26' 27", S 2° 9' 5" you should change the settings to decimal degrees. Geographic coordinates are used all over the world. Because they display the position on a globe, they have to be converted to a flat projection such as Universal Transverse Mercator (UTM) if you want to display them on a map.

- If you want to integrate your data into a Geographical Information System it can also be a good idea to already collect the data in UTM. UTM coordinates are referenced to 60 different UTM zones in the world. For example the UTM grid for Tuanan in Central Kalimantan is UTM Zone 50S. Coordinates in UTM look like this: Easting 215346.2, Northing 9761941.81 (same location as latitude/longitude above). However, if your project sites are far away from each other (more than 800km) and lie in different UTM zones it would be better to collect data in latitude/longitude and convert them later.

### *Collecting GPS data:*

- If you already know you will want to collect GPS data on a specific day (e.g. of a focal animal), turn on the GPS before you enter the forest and let it obtain a position while you stay stationary.
- When you arrive at the site (e.g. morning nest) wait at least 5 minutes before you record the first position. Like this, the GPS receiver has time to calculate your position more accurately.
- If you turn on the GPS inside the forest, wait until the indicator for position accuracy has stabilized, (usually around 10m).
- A GPS can store a number of points in its memory, but it is always better to note the coordinates and other relevant information on a separate sheet.
- When collecting GPS data while you are moving, try to stop and wait for at least 10 seconds or until the position isn't changing too much anymore before recording it.
- GPS positioning is not influenced by weather phenomena such as rain or clouds, but by canopy cover. Foliage, especially when wet, increases location error. On rainy days, put your GPS in a water-proof bag, but do not store it in your backpack, the wet cover will block the signal.
- When collecting GPS data, always hold your GPS upright so that the antenna has the most direct connection with the satellites in the sky. Some devices are designed for vertical use. Check in the user manual.
- Never put the GPS in your backpack and let it store data automatically inside the backpack. Try to always hold it upright before recording a location to obtain the best signal possible.

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## Annex 3 Individual orangutans' movement data

### Annex 3.1 Jinak

Year	Home Range Size (ha)	Core Area Size (ha)	Total observation points
2003	166.73	54.80	1736
2004	226.41	77.89	857
2005	131.37	48.64	2026
2006	195.96	70.19	1540
2007	167.11	43.65	1024

Annual ranges for Jinak

Seasons		Daily path length	Nest distance	Sinuosity index	Active Period (minutes)	Fruit feeding (minutes)	Vegetative matter feeding (minutes)
low FAI	Mean	626.66	380.44	1.86	662.66	303.70	87.83
	N	73	73	73	47	47	47
	Std. Dev	258.55	168.19	0.94	45.89	126.54	92.08
medium FAI	Mean	666.34	356.68	2.17	630.49	261.76	80.13
	N	93	93	93	89	92	93
	Std. Dev	396.06	174.06	1.60	54.75	117.34	76.76
high FAI	Mean	744.89	394.61	2.24	654.31	300.86	56.93
	N	73	73	73	70	70	71
	Std. Dev	262.32	175.27	1.42	48.46	86.44	56.46
Total	Mean	678.24	375.52	2.10	645.93	284.29	74.04
	N	239	239	239	206	209	211
	Std. Dev	322.35	172.68	1.38	52.36	111.56	75.23

Jinak's movement and behavioural data

	Test	F / Chi-Square	Sig.
Daily path length	Kruskal-Wallis	12.062	<b>0.002</b>
Nest distance	Kruskal-Wallis	2.282	0.319
Sinuosity index	Kruskal-Wallis	4.705	0.095
Active period	ANOVA	7.627	<b>0.001</b>
Fruit feeding	ANOVA	3.438	<b>0.034</b>
Vegetative matter	Kruskal-Wallis	3.315	0.191

Test for significance of differences

Annex 3.2 Juni

Year	Home Range Size (ha)	Core Area Size	Total observation points
2003	250.44	88.80	687
2004	358.34	130.94	888
2005	452.23	162.64	1197
2006	244.03	89.01	1384
2007	186.43	58.78	1379

Annual ranges for Juni

Seasons		Daily path length	Nest distance	Sinuosity index	Active Period (minutes)	Fruit feeding (minutes)	Vegetative matter feeding (minutes)
low FAI	Mean	739.00	413.21	1.97	660.73	286.08	114.23
	N	78	78	78	52	52	53
	Std. Dev.	411.80	235.48	0.92	55.56	140.67	110.11
medium FAI	Mean	955.18	534.15	2.69	660.85	303.80	79.07
	N	41	41	41	40	41	41
	Std. Dev.	398.38	317.48	3.72	61.73	121.27	72.85
high FAI	Mean	896.33	565.82	1.65	626.43	317.41	49.77
	N	44	44	44	44	44	44
	Std. Dev.	529.46	306.00	0.66	105.95	93.00	43.63
Total	Mean	835.85	484.83	2.06	649.67	301.45	83.23
	N	163	163	163	136	137	138
	Std. Dev.	450.90	284.54	2.02	78.12	121.06	86.52

Movement and behavioural data for Juni

	Test	F / Chi-Square	Sig.
Daily path length	Kruskal-Wallis	10.914	<b>0.004</b>
Nest distance	Kruskal-Wallis	9.699	<b>0.008</b>
Sinuosity index	Kruskal-Wallis	11.361	<b>0.003</b>
Active period	ANOVA	2.961	0.055
Fruit feeding	ANOVA	0.807	0.448
Vegetative matter	Kruskal-Wallis	6.452	<b>0.040</b>

Test for significance of differences

Annex 3.3 Kerry

Year	Home Range Size (ha)	Core Area Size (ha)	Total observation points
2003	126.99	49.60	400
2004	187.50	47.16	722
2005	304.67	86.09	1211
2006	217.65	61.51	1021
2007	330.30	101.45	1192

Annual ranges for Kerry

Seasons		Daily path length	Nest distance	Sinuosity index	Active Period (minutes)	Fruit feeding (minutes)	Vegetative matter feeding (minutes)
low FAI	Mean	657.26	386.79	1.786	622.45	244.19	109.71
	N	65	65	65	40	42	42
	Std. Dev.	333.29	196.064	0.54	73.36	125.24	88.27
medium FAI	Mean	1025.91	557.55	1.94	645.10	295.30	38.98
	N	44	44	44	40	43	43
	Std. Dev.	494.94	239.23	.87	58.69	73.84	37.97
high FAI	Mean	977.46	546.89	1.85	643.63	269.35	55.24
	N	35	35	35	32	34	34
	Std. Dev.	432.52	202.50	0.55	47.25	80.19	52.47
Total	Mean	847.73	477.88	1.85	636.59	269.85	68.59
	N	144	144	144	112	119	119
	Std. Dev.	445.23	225.95	0.66	61.94	98.28	70.45

Movement and behavioural data for Kerry

	Test	F / Chi-Square	Sig.
Daily path length	Kruskal-Wallis	20.708	<b>&gt; 0.001</b>
Nest distance	ANOVA	10.998	<b>&gt; 0.001</b>
Sinuosity index	Kruskal-Wallis	0.236	0.889
Active period	ANOVA	1.645	0.198
Fruit feeding	ANOVA	2.970	0.055
Vegetative matter	Kruskal-Wallis	21.201	<b>&gt; 0.001</b>

Test for significance of differences

Annex 3.4 Kondor

Seasons		Daily path length	Nest distance	Sinuosity index	Active Period (minutes)	Fruit feeding (minutes)	Vegetative matter feeding (minutes)
low FAI	Mean	827.85	367.66	2.58	644.90	224.62	154.00
	N	51	51	51	20	26	26
	Std. Dev.	311.43	183.94	1.18	48.82	119.19	84.06
medium FAI	Mean	1248.18	507.68	2.57	673.12	292.59	50.94
	N	17	17	17	16	17	17
	Std. Dev.	638.22	243.64	0.97	49.413	90.52	40.78
high FAI	Mean	2253.30	778.34	2.89	684.00	264.00	336.00
	N	1	1	1	1	1	1
	Std. Dev.	.	.	.	.	.	.
Total	Mean	952.07	408.12	2.58	658.16	251.77	118.32
	N	69	69	69	37	44	44
	Std. Dev.	474.92	211.11	1.12	49.91	111.43	91.61

Seasonal movement and behavioural data for Kondor

	Test	F / Chi-Square	Sig.
Daily path length	Kruskal-Wallis	8.393	<b>0.015</b>
Nest distance	Kruskal-Wallis	6.170	<b>0.046</b>
Sinuosity index	Kruskal-Wallis	0.547	0.761
Active period	ANOVA	1.612	0.214
Fruit feeding	ANOVA	2.009	0.147
Vegetative matter	Kruskal-Wallis	18.442	<b>&lt; 0.001</b>

Test for significance of differences

Annex 3.5 Mindy

Year	Home Range Size (ha)	Core Area Size	Total observation points
2003	86.56	28.05	611
2004	128.96	47.86	1103
2005	146.51	50.59	2068
2006	146.09	40.67	1061
2007	130.02	49.08	1866

Annual ranges for Mindy

Seasons		Daily path length	Nest distance	Sinuosity index	Active Period (minutes)	Fruit feeding (minutes)	Vegetative matter feeding (minutes)
low FAI	Mean	743.59	351.35	2.76	684.85	277.49	87.76
	N	77	77	77	39	39	41
	Std. Dev.	409.53	229.56	2.48	61.54	154.13	98.65
medium FAI	Mean	889.61	450.73	2.16	671.92	294.48	66.96
	N	54	54	54	52	54	54
	Std. Dev.	418.39	193.41	1.28	61.28	110.90	56.10
high FAI	Mean	944.90	471.00	2.19	696.68	332.27	53.37
	N	62	62	62	59	60	60
	Std. Dev.	365.05	191.51	0.919	35.92	83.51	52.96
Total	Mean	849.12	417.59	2.405	685.02	304.97	67.20
	N	193	193	193	150	153	155
	Std. Dev.	406.12	214.07	1.80	53.54	116.02	69.80

Seasonal moement and behavioural data for Mindy

	Test	F / Chi-Square	Sig.
Daily path length	Kruskal-Wallis	13.164	<b>0.001</b>
Nest distance	Kruskal-Wallis	6.630	<b>0.002</b>
Sinuosity index	Kruskal-Wallis	1.852	0.396
Active period	Kruskal-Wallis	5.205	0.074
Fruit feeding	ANOVA	3.056	0.050
Vegetative matter	Kruskal-Wallis	2.194	0.334

Test for significance of differences

Annex 3.6 Sumi

Year	Home Range Size (ha)	Core Area Size	Total observation points
2004	171.65	56.06	1547
2005	166.46	53.14	1209

Sumi's annual ranges

Seasons		Daily path length	Nest distance	Sinuosity index	Active Period (minutes)	Fruit feeding (minutes)	Vegetative matter feeding (minutes)
low FAI	Mean	661.47	401.82	1.81	649.86	237.71	108.73
	N	30	30	30	28	28	30
	Std. Dev.	177.26	145.85	0.78	46.59	143.95	86.65
medium FAI	Mean	573.42	310.96	2.23	643.71	247.51	119.02
	N	45	45	45	45	45	45
	Std. Dev.	258.42	156.59	1.46	51.15	99.27	69.41
high FAI	Mean	738.53	359.60	2.52	654.42	300.73	86.36
	N	66	66	66	64	66	66
	Std. Dev.	326.47	194.44	1.95	47.38	82.39	50.55
Total	Mean	669.44	353.06	2.28	649.97	270.81	101.55
	N	141	141	141	137	139	141
	Std. Dev.	286.72	175.40	1.62	48.37	105.93	66.89

Movement and behavioural data for Sumi

	Test	F / Chi-Square	Sig.
Daily path length	ANOVA	4.685	<b>0.011</b>
Nest distance	ANOVA	2.557	0.081
Sinuosity index	Kruskal-Wallis	2.252	0.324
Active period	Kruskal-Wallis	1.437	0.487
Fruit feeding	ANOVA	7.982	<b>0.001</b>
Vegetative matter	Kruskal-Wallis	5.364	0.068

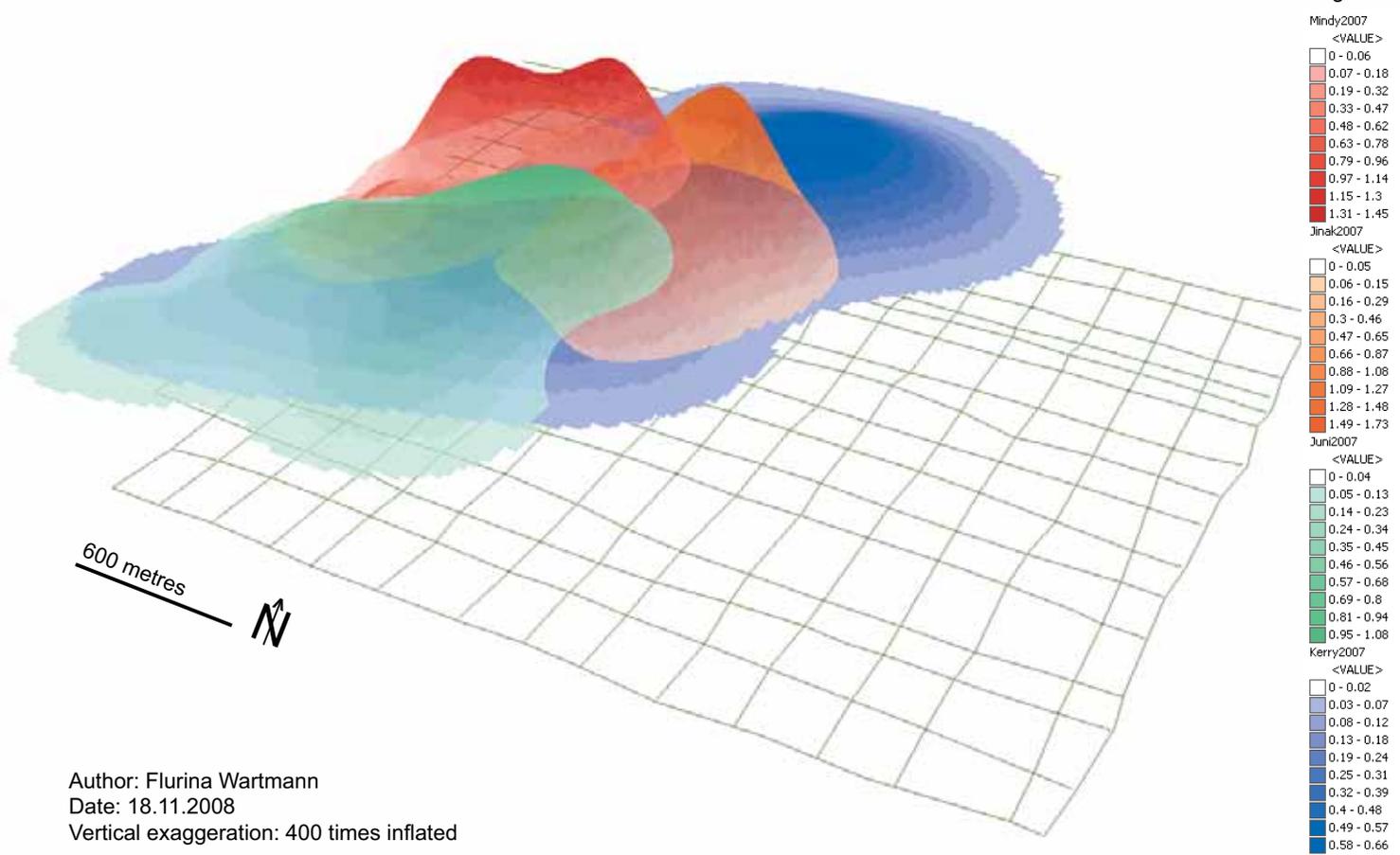
Test for significance of difference

Annex 4 Correlation matrix

			Fruit feeding	Active period	Vegetative feeding	Nest distance	Travel distance	Sinuosity index	Fruit Availability
Spearman's rho	Fruit feeding	Correlation Coefficient	1.000	.290(**)	-.493(**)	.139(**)	.144(**)	-.040	.168(**)
		Sig. (2-tailed)	.	.000	.000	.000	.000	.258	.000
		N	805	783	805	805	805	805	805
	Active period	Correlation Coefficient	.290(**)	1.000	-.194(**)	.304(**)	.513(**)	.229(**)	.029
		Sig. (2-tailed)	.000	.	.000	.000	.000	.000	.419
		N	783	783	783	783	783	783	783
	Vegetative feeding	Correlation Coefficient	-.493(**)	-.194(**)	1.000	-.295(**)	-.352(**)	.002	-.233(**)
		Sig. (2-tailed)	.000	.000	.	.000	.000	.963	.000
		N	805	783	813	813	813	813	813
	Nest distance	Correlation Coefficient	.139(**)	.304(**)	-.295(**)	1.000	.703(**)	-.435(**)	.195(**)
		Sig. (2-tailed)	.000	.000	.000	.	.000	.000	.000
		N	805	783	813	970	970	970	970
	Travel distance	Correlation Coefficient	.144(**)	.513(**)	-.352(**)	.703(**)	1.000	.254(**)	.225(**)
		Sig. (2-tailed)	.000	.000	.000	.000	.	.000	.000
		N	805	783	813	970	970	970	970
	Sinuosity index	Correlation Coefficient	-.040	.229(**)	.002	-.435(**)	.254(**)	1.000	-.002
		Sig. (2-tailed)	.258	.000	.963	.000	.000	.	.954
		N	805	783	813	970	970	970	970
	Fruit Availability	Correlation Coefficient	.168(**)	.029	-.233(**)	.195(**)	.225(**)	-.002	1.000
		Sig. (2-tailed)	.000	.419	.000	.000	.000	.954	.
		N	805	783	813	970	970	970	970

\*\* Correlation is significant at the 0.01 level (2-tailed).

### 3D Visualization of kernel ranges for orangutan females in 2007



Author: Flurina Wartmann  
 Date: 18.11.2008  
 Vertical exaggeration: 400 times inflated