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Modelling socio-spatial movement behaviour of orangutans (Pongo abelii) in Suaq (Sumatra Utara)

GEO 511 Master's Thesis

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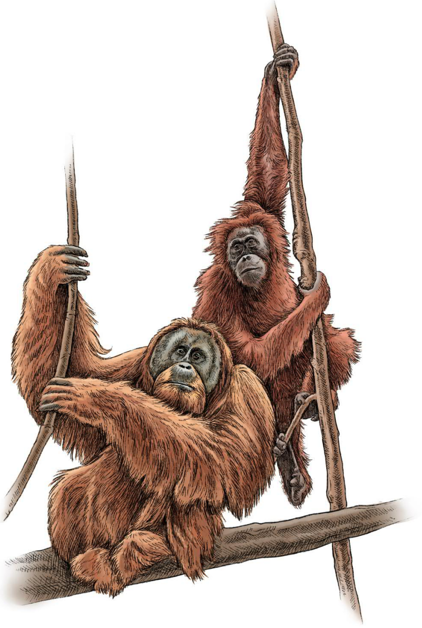

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Summary

The Sumatran orangutan (*pongo abelii*) is a flagship species for its valuable tropical rainforest habitat, but they are critically endangered. Habitat loss and wildlife trade can bring this close relative of ours to the brink of extinction. As humans continue to remove land from its natural habitat, the spatial behavior and needs of orangutans are of particular interest. The spatial behaviour and ecology of orangutans and their ecological needs are still poorly understood. By looking at different habitats and populations, the influence of external and internal factors on orangutans can be analysed. A data set from Suaq (Sumatra Utara, Indonesia) was compared to the available literature of a second research site in Tuanan (Borneo, Indonesia). The habitats and their topography are very similar, but fruit productivity, density, and sociability are much higher in Suaq which allows us to compare the underlying ecological differences.

Three spatio-temporal levels of analysis were defined: Level 1 - distance patterns, Level 2 - daily movement patterns and Level 3 - momentary movement behaviour. In the context of this work, mainly level 1 and level 2 were analysed. For the first level, the focus was on ten adult females, while for the second level results for all age and sex classes were included. For all further analyses, external and internal predictors were used to see how they influenced the movement patterns found. External factors were Fruit Availability Index, average temperature, daytime and nighttime rainfall, and a derived density of fruit tree value. Internal factors for all individuals were age-sex classes. Whereas for adult females – which were the focus of this thesis – dominance rank, age, age of current offspring and relatedness were considered.

On level one, the ranging pattern over the full study period and some user-defined periods were analysed with four home range algorithms (Minimum Convex Polygon, Kernel Distance Estimation, Biased Random Bridge, Autocorrelated Kernel Density Estimation. KDE and BRB gave similar estimates and proved to be the most useful. They did not over-smooth or under-smooth the distribution and were of high quality with respect to the defined quality descriptors (e.g. number of polygons, compactness, number of holes and Area Under the Curve). The AKDE was useful to access the absolute home range sizes for smaller sample sizes and the MCP was mainly used to compare the results with other studies. The unbalanced data set in terms of time and size proved to be the main problem in analysing spatial behaviour with the present data set. A conservative approximation of about 100 animals was determined, leading to reliable range estimates. Home ranges were found to be ranging between 1.6 (algorithm: BRB, focal: Ellie) and 2.4 km^2 (algorithm: BRB, focal: Cissy) which is smaller than in recent studies. Likewise were core ranges smaller than expected but seemed more stable and less dependent on sample size. Existing hypotheses that home ranges in Suaq are much bigger based on the patchiness of feeding resources than, e.g. in Tuanan could not be confirmed. Dominance, age and the number of normalised forage trees were found to have no effect on the size of the home ranges. Fruit trees can account for some larger core ranges, but in general, the normalised fruit tree value did not differ between overlaps, core ranges nor complete home ranges. The overlaps of the resulted home ranges were also compared with different algorithms. The Utilization Distribution Overlap Index (UDOI) was especially useful in estimating overlaps based on the uncertainty analysis conducted at the beginning of this thesis. Overlap percentages of home ranges were bigger than for core ranges which may indicate partial range exclusion. The total amount of relatively shared range was found to be on average 84% and for core ranges 96%. However, using the UDOI values ranged between 0.32 (focal: Yulia) and 0.7 (focal: Tiara) where 1 equals 100% overlap. Relatedness explained around 10% higher overlaps and similar dominance levels showed to explain lower values of overlaps. The higher overlap of related females may be the result of female philopatry rather than a sign of active range exclusion. The higher overlap of differing dominance rank groups may result from the enlarged home ranges of young females.

On level two, 1314 follows were mainly analysed by deriving the Day-journey-length or daily total-traveled-distance (DJL) and two tortuosity indices namely, the Straightness Index (SI) and the sinuosity index. A preliminary analysis revealed that an underestimation of DJL is present, based on the chosen sampling interval. DJL was around 35% lower when GPS fixes were taken every 30 min instead of every 5 min. The discussion of how much DJL actually reflect real daily movement, which revealed that many uncertainties exist and that further research is needed (e.g. denser sampling interval, inclusion of height changes).

Nonetheless, the average DJL of 885 m was found to be higher in Suaq than in Tuanan. The overall higher travel distance is mainly addressed to a more pronounced "search and find“ strategy compared to a ”sit and wait“ strategy in Tuanan during seasons of low fruit availability. Especially flanged males tended to travel much further in Suaq (+200 m) than in Tuanan, even slightly more than adult females. Flanged males in Suaq may adjust their mating and movement strategies based on habitat productivity and social conditions. The more stable dominance hierarchy between males may be maintained by longer DJL of flanged males. This results in the greater risk of unflanged males becoming flanged males and the greater developmental arrest in Suaq compared to Tuanan can be explained.

External factors like day rain and night rain, average temperatures and fruit availability did not show any impact on day journey length. This indicates a ceiling effect where fruit availability is always high enough to support high movement activities, even when variation in FAI occurs. For females, dominance did not impact the movement parameters but the age of the current offspring did. The DJL increased from around 800 m to 1000 m on average over the duration of motherhood (for every year +34 m). A very similar pattern was also found in Tuanan and probably relates to the clinging of young offspring at lower ages but also to an adjustment to the offspring's energy, household and movement competence. The age of the current offspring also influenced both tortuosity indices negatively (negative in the sense of tortuosity) and showed that I actually can detect movement changes with these indices. The only other factor which explained tortuosity was the number of visited fruit trees. This could indicate that feeding tree distribution is actually slightly clumped.

Furthermore, this thesis gives various backgrounds and further insights into the available data set and possible future research. E.g. about the movement activity over daytime (level 3). The immense effort of preparing the analysis and the data set is additionally described and the used methods implemented in R are openly available.

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- Finally, I would especially like to thank all voluntary participants in the Indonesian rainforest for agreeing to be tracked and observed for over ten years.

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List of Acronyms

AKDE	Autocorrelated Kernel Density Estimation
AUC	Area Under the Curve
BA	Bhattacharyya Affinity
BCV	Biased Cross-Validation
BRB	Biased Random Bridge
CR	Core range
DJL	Day-journey-length or daily total-traveled-distance
DOP	Dilution of Precision
ENSO	El Niño–Southern Oscillation
FAI	Fruit Availability Index
FL	found-to-lost
FN	found-to-nest
HDOP	Horizontal Dilution of Precision (2D)
HR	Home Range
HRE	Home Range Estimator

ICC	Intraclass Correlation
KDE	Kernel Distance Estimation
LMM	Linear Mixed Model
MCP	Minimum Convex Polygon
NL	nest-to-lost
NN	nest-to-nest
PI	Solve-the-Equation Plug-In
PVA	Population Viability Analysis
REF	Reference method
SCV	Smoothed Cross-Validation
SI	Straightness Index
SOI	Southern Oscillation Index
SST	Oceanic Niño Index
TDD	Total Displacement Distance
UD	Utilization Distribution
UDOI	Utilization Distribution Overlap Index
VI	Volume of Intersection
VIF	Variance Inflation Factor

Glossary

age-sex classes	The age-sex classes are as followed: infants (dependants), male and female independent immatures (juveniles, sometimes adolescents, nulliparous females), flanged males, unflanged males (both sexually active) and adult females (mostly mothers).
day journey length	The term daily travelled distance is often used in ecological studies. In orangutan studies the term day journey length was introduced by describing the daily travelled distance between morning nest and night nest.
focal	In terms of orangutan standardized field methods the observed orangutan which will be followed is designated as focal.
philopatry	Natal philopatry describes a phenomenon in many animal species where offspring often settle or bread spatially close to their parents.

scramble competition	In terms of ecology it describes a competition around resources which are accessible to all competitors.
total displacement distance	The term refers to the euclidean distance between the morning nest of an orangutan and the night nest of an orangutan.

Chapter 1

Introduction

1.1 Background

The digital revolution also did not halt of the field of animal ecology. Nowadays, an ever-increasing number of tools are available to track, analyse and observe our natural surroundings. In new global cities, digital twins of a city are intended to serve as a basis for analysing the state and functioning of the urban system. In spatial ecology, digital tools are increasingly used to model complicated ecological cycles and inferences. Remotely sensed ecological data, machine learning, deep learning, data mining and three-dimensional models of ecosystems are examples of advancing methods in spatial ecology (D'Urban Jackson et al., 2020).
The availability of movement data of animals is increasing intensely. Especially the 2007 initiated Movebank project of the Max Planck Institute of Animal Behaviour boosted the research in this area (Mrozewski, 2018). A long-term study of movement is also conducted at the Department of Anthropology of the University of Zurich. They observe orangutans in the peat swamp forests in the Leuser Ecosystem on the Indonesian Island of Sumatra. The name of the research station is Suaq Balimbing. This study uses handheld GPS data from Suaq sampled from orangutan locations in the peat swamp forest of Sumatra, Indonesia. This thesis aims to add insights to the already existing work about socio-spatial movement patterns of orangutans. I give a good understanding of the available GPS data set and its future use by offering various results about orangutans' spatial behaviour. Moreover, the limits of available data resolution and its expressiveness are discussed.

1.2 Motivation – Conservation

Orangutans are the largest arboreal mammal and one of humans' closest relatives (Parsons 1999). Hence, it does not surprise that "orangutan" means "forest-human". Furthermore, orangutans are a key flagship species in biodiversity conservation terms. The close relationship between humans and orangutans, and the simultaneous portrayal of this close relationship in zoos, films and media through the humanisation of this animal, leads to the emotional reaction of the public in wilderness conservation campaigns (Jepson and Barua, 2015) and even recently seen in political campaigns in Switzerland as symbolic representations for and against the Comprehensive Economic Partnership Agreement between the EFTA States and Indonesia. Nevertheless, all three described orangutan species are on the Red List of Critically Endangered Animals (Singleton et al., 2018). Especially habitat loss and wildlife trade could bring this species to the brink of extinction. In Marshall et al. (2009) a Population Viability Analysis (PVA) was conducted for the last remaining orangutan populations in Sumatra and Borneo. They found that the minimum viable population size is >250 individuals to maintain a genetically healthy population. The risk of extinction is mainly determined by the number of individuals living in an isolated population habitat. A smaller population has a higher risk of extinction than a larger one. In addition, large-breed animals' (> 3 kg), slow reproductive rate, limited geographical extent and frugivory have been described as extinction-promoting factors. Orangutans have the slowest reproductive rate of all terrestrial mammal, making them particularly vulnerable to extinction (Marshall et al., 2009). In their PVA for Sumatra, Marshall et al. (2009) further predicted a 50 % population decline over the next 50 years based on realistically assessed deforestation rates and life history parameters. Of the 15 populations considered, only 5 will have enough individuals (< 250) to maintain a constant population and sufficient space for suitable habitat. According to this model, the extinction of Sumatran orangutans occurs within 300 years if no measures are taken to halt habitat destruction and promote habitat conservation. These modelled results give us an idea of how stable the current orangutan populations most likely are and how the populations' extinction might look. One of the key observations from Marshall et al.'s paper is that fragmentation and isolation significantly negatively affect population size. Nevertheless, this effect is temporally delayed and only visible when it is too late. Therefore, population estimates, e.g. by remote nest counting, may not be sufficient to predict the future population decline (Marshall et al., 2009).

First, even though great efforts are made to protect orangutans, many aspects of their behaviour and ecology remain poorly understood. And yet, those factors are important to understand the species' ecological needs. To understand these needs, the analysis of socio-temporal behaviour, e.g. under different environmental conditions, can help understand how orangutans cope with a changing environment (climate, diet availability) or the destruction of their habitat. A detailed analysis of how habitat functions and space are used can shed light on new approaches for estimating orangutan populations in an unknown habitat or complement the understanding of existing population estimates. This is crucial to develop appropriate conservation measures to protect this close relative of ours as a flagship species for the entire Southeast Asian forest ecosystem located in the biodiversity hotspot of the Sundaic region (Brockman and Van Schaik, 2005; de Bruyn et al., 2014; Jepson and Barua, 2015).

Therefore, this project helps to lay the foundation for more evidence-based orangutan conservation based on the knowledge about influencing environmental and inter-social factors. Second, there is a need for adding insights to the already existing movement models for arboreal primates. Because many effects of moving in an arboreal habitat remain unclear (McLean et al., 2016). This is not only important to understand the behavioural and social aspects of orangutans but to understand important seed dispersing functions which are of big interest for rainforest ecology. And third, orangutans are a highly social animal. Understanding the origin of spatial planning, differences between sex classes in their movement behaviour and the social-spatial movement behaviour, new insights could be gained from analysing the GPS-data sets of this close relative of ours.

1.3 Comparing studies and research gaps

Investigating how much space orangutans use, how much their ranges overlap with other individuals, what factors affect orangutan ranging behaviour on different levels (Section 1.5) is, as already said, crucial for developing effective and long-term conservation strategies. Few studies focused on the spatial analysis of orangutan survey data sets. Even fewer studies used newer home range algorithms to approximate space use and female avoidance or tolerance, respectively (Table 1.1). Mostly they focused on answering more qualitative research questions about orangutan behaviour (Wich et al., 2009). The first mainly spatial analysis about orangutans is by Singleton and Van Schaik (2001) where the main goal was to approximate home range sizes for three females, three adult males and three subadult males. Methodologically, the locations of orangutans were taken by marking them on a paper map with the research area transect network as a guide for orientation. Wartmann (2008) showed that around 80 % of the location points drawn on maps lay within 25 m of the location measured by GPS devices, and inaccuracies of map drawn points mostly result from mistakes by the follower. Nonetheless, studies using maps instead of GPS are very meaningful, and including old data sets that only used maps could be an asset, especially when long-term observation increases expressiveness. This is especially the case when analysing home ranges (Chapter 4). Singleton and Van Schaik (2001) used four approaches to extract total home range sizes, a rough and a fine-scale grid count method, summing up all GPS-Points under a grid, a Minimum Convex Polygon method for 100 % of points and a circle method which uses a circle around the centre of all points. They found that most individuals have a large and stable home range, except subadult males who tend to travel far and do not stay in a fixed range. This corresponds to the expectation that range use in males is basically a response to female distribution (Setia et al., 2009a). Age-sex class is therefore playing a big role in explaining home range sizes. Accordingly Knott et al. (2008) have done a similar study with the same methods in Gunung Palung, Borneo while focusing on female-female competition. They similarly found stable and highly overlapping home ranges of up to 90 % per individual. They argued that there must be a form of avoidance and competition over resources and discussed that core home ranges may be actively defended while in other areas there is a passive exclusion competition (Section 1.6). Singleton and Van Schaik (2001) further showed that females mostly used a core range very frequently, although they travelled within much larger areas. The four methods used to calculate the total home range sizes differed significantly. Their results also showed an unexpectedly large average home range for the population in Suaq and a very high density of home range overlaps, which corresponds to the high density of orangutans found in Suaq (Singleton and Van Schaik, 2001). The factors underlying these large home ranges and the high density of orangutans living in Suaq were mainly related to habitat properties. Sumatran orangutans occur in higher densities, probably due to higher plant productivity, where peat-swamp forests additionally showed higher support of individuals. Other discussed influences on density and home range size are altitude, disturbances by humans (e.g. hunting or logging, interdependent as well) and mosaic-like sites with multiple spatially distinct habitat types (Husson et al., 2009; Marshall et al., 2009).

Flurina Wartmann and Alison Ashbury carried out further analyses of orangutan spatial behaviour. Both worked with data from Tuanan, a research site in Borneo which has a very similar habitat to Suaq (disturbed secondary peat swamp forest). However, there are key differences, one being the researched species and their corresponding difference in behaviour, e.g., less sociability in *pongo pygmaeus* and lower degree of arboreality. The lower sociability has a variety of effects on many other behavioural aspects and differences between sites. For example, opportunities of social learning are a much more important aspect in an orangutan's development. In Suaq we find an overall higher diet complexity which probably also promotes the use of tools, a unique skill only found in Suaq (Schuppli et al., 2016). Furthermore, the peat swamp forest of Tuanan has half the orangutan density (3.84 individuals per km^2) compared to the peat swamp forest of Suaq (7.2 individuals per km^2) (Husson et al., 2009; Wich et al., 2009). A main aim of this thesis is therefore to analyse if we can find similar effects of explanatory variables on movement patterns as they were found in Tuanan.

Wartmann (2008), who comes originally from the field of GIScience, focused on multiple spatial parameters derived from GPS and digitised locations. She used different home range algorithms as well as DJL to investigate the influence of seasons on the orangutans' spatial behaviour. She used Kernel Distance Estimation (KDE) for approximating home ranges, which was not used for orangutans before and found it to be more appropriate than MCP because the sample size was less important and sizes of home ranges were more reliable (for more information about home range algorithms, Chapter 4). The main findings of her study were that home ranges of females remained stable over years and that bigger home ranges did not mean that orangutans travelled further per day. Using advanced modelling techniques Alavi (2018) on the contrary found evidence of higher DJL when home range size was bigger, although this did not mean that home range crossing times were faster. He argued that home range crossing times are influenced by the tortuosity of movement. He measured tortuosity as the autocorrelation of velocity and found no difference between sex classes.

Wartmann (2008) found total displacement distance (TDD) and the day journey length (DJL) was highly dependant on the individual. Fruit availability (seasonal mast fruiting events) in Tuanan was found to positively impact the DJL and even maybe the home range size, as did sexual activity (Wartmann, 2008). The relationship of FAI and DJL in Tuanan was further analysed by Vogel et al. (2017). They found differences between the daily travelled distance for the age-sex classes (Table 1.1). Active period which could explain longer DJL did not differ enough to explain such a variation. FAI had a big effect on DJL for all age-sex classes. The DJL increased approximately by 60 m per increase of 1 (equals to 1 percent of trees fruiting) in FAI. Again, the active period did not change with higher DJL, except for immature females. Generally, immature females showed the highest values for DJL, which reflects the findings by van Noordwijk et al. (2012) and Ashbury (2013) who already described the higher activeness of immature females during a phase of exploration and establishing a home range (Vogel et al., 2017). Alison Ashbury analysed female philopatry of orangutans in Tuanan by exploring their home ranges in different stages of their life. She found that home ranges tended to be stable in size and across locations, but maturing females showed a phase of exploration where home range size and DJL increased.

This thesis tries to fill a gap in describing and formalizing the movement behaviour of orangutans for Suaq which was likewise done in Tuanan. Therefore, we compare the results found by Ashbury et al. (2020) and Wartmann et al. (2010) with the findings of this thesis. This thesis is therefore partially a reproduction of previous studies done in Tuanan, however, with a different species and in a different location with vastly unequal characteristics, and also with the introduction of some new methodologies in orangutan research. Additionally, we try to gain new insights about specific influencing variables such as feeding trees, weather and relatedness. There are mainly six different age-sex classes: adult females, two adult male morphs; flanged males, unflanged males, immature females, immature males and infants (Thorpe and Crompton, 2006) (for further information about age-sex classes Section 1.6). The main focus of this thesis is on female orangutans, for the latter part, because generally, male ranging sizes are expected to be too big to get reasonable results due to the research area size limits (Singleton and Van Schaik, 2001). For the first part about movement parameters (Chapter 4), we will include results for males as well, but for females we include further explanatory variables such as the age of the offspring, the age and the dominance category.

Table 1.1 – Overview of spatial behaviour studies and their methods and results. The location, the orangutan species analysed, the results and their level of analysis, and their corresponding method were reported.

Source	**Location,** **habitat mosaic,** **habitat type**	**Study duration,** **Study area,** **Orangutan density,** **Sampling interval** **Subject**	**DJL [m]** **Straightness Index**	**Home range (HR)** **Core range (CR)** **[km^2]**	**Overlap** **% shared total: $\sum$ (A ∩ .. / A)** **% shared dyadic: (A ∩ B / A)** **% to dyadic HR sum: (A ∩ B) / (A ∪ B)** **dyadic overlap: (A ∩ B / A)*(A ∩ B /B)**
Singleton et al. (2001) Singleton et al. (2002) Singleton et al. (2009)	Suaq Balimbing (abelii) Homogenous Peat swamp, freshwater swamp, hill dipterocarp	48 months (Jun. 1994 - Sept. 1998) 5-20 km^2 7 focal/km^2 30 min All age sex classes	**DJL** Adul. female: 833±306 Sexually active females: 1077±368	**HR** Adul. females MCP$_{100\%}$: 6.99 Adul. females Grid cell 100m: 2.72 Adul. females Grid cell 200m: 4.81 Fl. males MCP$_{100\%}$: 9.1 Fl. males Grid cell 100m: 1.67 Fl. males Grid cell 200m: 3.2 Unfl. males MCP$_{100\%}$: 4.76 Unfl. males Grid cell 100m: 1.16 Unfl. males Grid cell 200m: 2.28 **CR** Adul. females MCP$_{50\%}$: 0.5 Yearly MCP$_{100\%}$ are 49% of the MCP$_{100\%}$ of the full period (male ranges exceeded study area, strong underestimation!)	"16 individuals, strong overlapping HR"
Wartmann et al. (2009, 2010)	Tuanan (morio) Homogenouspeat swamp	52 months (2003 - 2007) 5 km^2 4.2 focal/km^2 30 min (some are drawn) Oenly females	**DJL** 777.21±402.39 m (n = 972, min = 84 m, max = 2691 m) **SI** 0.47	**HR** MCP: 2.79 Grid cell 50m: 2.2 Grid cell 25m: 1.21 KDE$_{95\%}$ fixed : 2.57 (yearly) **CR** KDE$_{50\%}$ fixed : 0.65 "Generally 1/3 of 95% HR" (yearly)	39 ± 21% (KDE$_{95\%}$ fixed, full study period, shared total)
Noordwijk et al. (2012)	"	84 months (July 2003- July 2010) 5 km^2 4.2 focal/km^2 30 min Only females	-	**HR** KDE$_{95\%}$ fixed (BCV) : 3.27.5±1.247 **CR** KDE$_{50\%}$ fixed (BCV) : 0.840 ± 0.276	Relatives: HR 57.32% , CR 15.79% Not relatives: HR 36.90%, CR 6.85% (KDE yearly, shared dyadic)
Vogel et al. (2016)	"	108 months (July 2003- July 2012) 5 km^2 4.2 focal/km^2 30 min All age sex classes	**DJL** Unfl. male: 888.5±36.27 (n = 206) Fl. male: 668.45±32.25 (n = 202) Adul. female: 778.77±10.98 (n = 1280) Immat. male: 812.61±64.82 (n = 38) Immat. female: 1040.32±27.61 (n = 367)	-	-
Ashbury et al. (2020) Ashbury (2013)	"	168 months (2003-2017) 5 km^2 4.2 focal/km^2 30 min Only females	**DJL** Daughters: 882±425.2 m (min = 147, max = 2550 m, n = 688) Mothers: 726±361.4 m (min = 72, max = 2176 m, n = 1294)	**HR**: KDE$_{95\%}$ fixed daughters: 2.65±1.098 (0.92 to 4.60) KDE$_{95\%}$ fixed mothers: 2.39±0.963 (1 to 4.3)	0.56 (0.13 to 0.98) (KDE for each age phase, dyadic overlap)
Digiorgio et al. (2012)	Gunung Palung (wurmbii) Heterogenous	34 months (Nov. 2008 – Aug. 2011) 21 km^2 3 focal/km^2 30 min Only females	-	**HR** MCP$_{100\%}$: 2.16	86.5% (28.32% – 99.32%) (MCP, full study period, shared total)
Knott et al. (2008)	"	104 months (Aug. 1994 – Apr. 2003) 21 km^2 3 focal/km^2 30 min Only females	-	**HR** Grid cell 100m: 3.73 Grid cell 200m: 5.08 MCP$_{100\%}$: 5.95 **CR** MCP$_{50\%}$: 0.65 ("13% of 95% HR")	-
Campbell et al. (2011)	Batang Serangan area (abelii) Heterogenous Human transformed, agroforest, degraded forest, bisected by palm oil, rubber, subsistence crops (jackfruit, durian, jengkol, petai)	24 months (Feb. 2007 - Feb. 2009) 32.34 km^2 - 30 min All age sex classes	**DJL** 867 m **SI** 0.34	**HR** MCP females: 1.31 MCP males: 4.23 Grid cell 100m females: 1.65 Grid cell 100m males: 2.03 KDE$_{95\%}$ fixed both: 3.275±1.247 KDE$_{95\%}$ fixed females: 2.14 KDE$_{95\%}$ fixed males: 3.88	female1 and female3: 17% female 2, female 4, female 5: 90% male 1, male 2, male 3: 89% (MCP yearly, dyadic sum.)

1.4 Structure of this thesis

The remainder of this first Chapter is devoted to providing definitions of movement patterns in orangutans (Section 1.5). This is then followed by Section explaining some of the behavioural aspects of orangutans, especially in relation to our research questions 1.6. The idea is to present all the relevant background information from orangutan ecology, life history, and sociability to comprehend and interpret the movement behaviour for the following chapters and for the research questions. In the last section of this first Chapter I will outline my research questions and state my hypotheses (Section 1.7). The second Chapter of this Master thesis aims to give a general introduction to all relevant information about the data processing, the data set and the study area as well as the methodologies used (Section 2.2.1). Moreover, this second Chapter already shows some simple data results to understand and visualise the additionally used data sets such as weather, fruit availability, and so on (Section 2.2). Furthermore, a quick analysis of the researcher bias will be presented and immediately discussed (Section 2.2.3).

The second part of this Masterthesis consists of the Introduction, Analysis, Results and Discussion of my research questions. This second part is subdivided into two main focuses of analysis and two main Chapters. First, I will analyse orangutans' daily movement (Chapter 3). Therefore, the widely used concept of DJL, sinuosity index and SI are used to analyse influential factors on these movement parameters. These parameters are legitimate descriptors of movement behaviour and were already used in various studies of primates and orangutans (Benhamou, 2004; Schuppli et al., 2016; Seidel et al., 2018). Second, a research of the orangutans spatial distribution will be done (Chapter 4). Hence, we use the concept by Burt (1943) and define it for our purpose. Further we use different home range algorithms to discuss different results of these spatial algorithms but also to allow us to oppose our results to previous results from Tuanan and Suaq. Although these two foci are somewhat interwoven, it makes sense to separate them in this thesis and combine them only in some specific parts, for example in future research about specific research questions of *pongo abelii*'s movement behaviour.

The third part of this thesis tries to conclude this research by comparing it to studies done using the data set collected at the Tuanan field site (*Pongo pygmaeus wurmbii*).

1.5 Definition of movement and levels of analysis

So far, spatial analysis of orangutans mostly focused on home ranges, even if individual trajectories were available (Campbell-Smith et al., 2011; Singleton and Van Schaik, 2001; Wartmann et al., 2010; Wich et al., 2009). Therefore, analysing and modelling orangutan trajectories has only been done in a handful of studies, although the movement patterns are interesting and also important for an adequate home range analysis (Wartmann, 2008). There is a lack of clear definitions when analysing trajectorial, spatial movement data of orangutans. The movement space, as well as the movement trace, has to be well defined (Laube, 2014). This means that it is very important to define the possibilites and properties of movements. The definition presented below fits in with the literature, without dividing into different fields but, well defines common aspects of animal movement (**RQ A.1**).

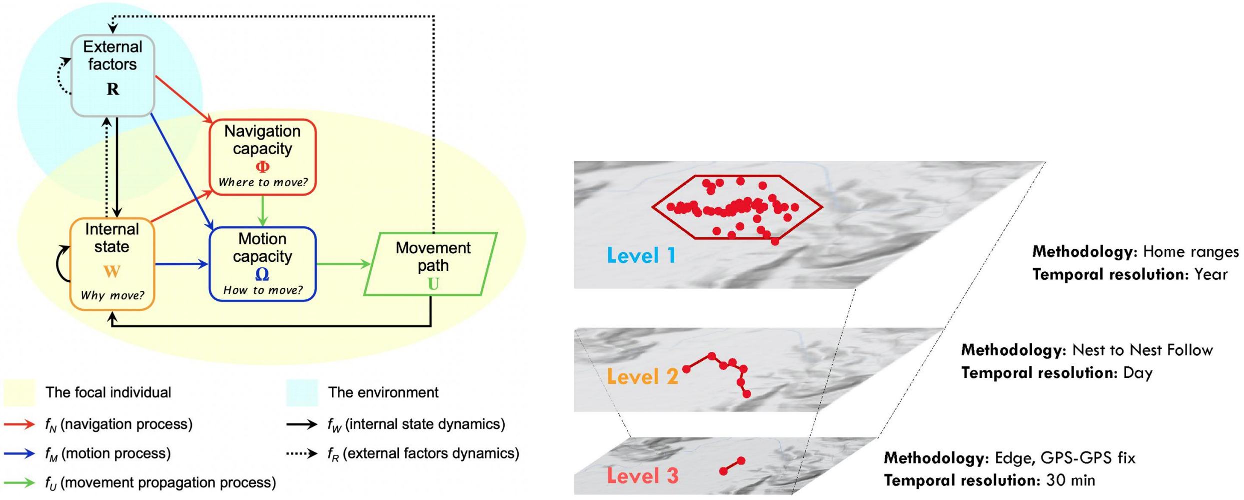
Nathan et al. (2008) criticised the differentiation of various movement studies by different taxa, geographical areas and research fields. A specific example, in the field of orangutan ecology is the concept of tortuosity, which was used or mentioned in a limited number of studies about orangutan movement before (Ashbury, 2020; Schuppli et al., 2016; Wartmann, 2008). However, several studies did not offer a clear definition of the term or did not use consistent terminology. Such sinuosity indices are well studied in computational movement analysis Benhamou (2004); Seidel et al. (2018) and therefore it could be helpful to use these concepts, for example to find more appropriate tortuosity measures for the forest habitat. Generally, uncertainties of sampling interval, properties of movement space, as well as exact properties of movement behaviour are frequently mentioned but not defined and analysed.

The following definition is based on the book of computational movement analysis by Laube (2014), the defined levels of movement parameters in the paper of Seidel et al. (2018) and the concept of universal movement aspects of Nathan et al. (2008).

Definition of movement model

Due to trees, the movement space in forests has a three-dimensional property. Movement along branches is the main movement of the arboreal orangutan; the movement space can therefore be seen as limited or partially constrained and the derived movement data within this space are perceived best by the Lagrangian model (movements are tracked, not fixed passings such as camera traps or sightings) Laube (2014). Although the canopy structure is quite permeable and orangutans are able to move on the ground, the space is not as uniformly accessible as it seems and many challenges while moving through the canopy have to be overcome (Cant, 1992). Manduell et al. (2012) state that the canopy architecture of a habitat has an effect on orangutans' locomotion, which does not necessarily mean that the movement is influenced as well. But they also hold that pathways through larger trees were observed more often in Suaq than expected and usage of similar pathways was observed. This is also supported by Davies et al. (2017b), who showed that movement of orangutans can best be expected towards canopy closures and tall trees, simultaneously avoiding canopy gaps and moving toward emergent crowns. Manduell et al. (2012) states no age-sex differences were found in using similar or more different pathways (Manduell et al., 2012). However, Chappell et al. (2015) studied gap crossing and found that the required techniques were correlated with physical and cognitive development. This means that gaps with their weak canopy support indeed influence the movement of age-sex classes differently. They found that the size of gaps increases with body size, albeit the ratio of body size to gap sizes decreases with body size Chappell et al. (2015). Looking at the movement paradigm by Nathan et al. (2008) the tree environment and the individuals' capacities can therefore have a significant impact on the movement path of an animal (Figure 1.1a). Many external influences, such as seasonality and distribution of food sources, forest structure, and population density showed to influence the movement pattern of orangutans (Ashbury et al., 2020; Wartmann et al., 2010). Furthermore, many individual internal factors play a role, such as age-sex classes, life phases, and relatedness, as it was seen in various studies where the individual was always an important variable with high significance in explaining spatial patterns (Alavi, 2018; Ashbury et al., 2020; Knott et al., 2008; Singleton and Van Schaik, 2001; van Noordwijk et al., 2012; Wartmann et al., 2010).

Nathan et al. (2008) proposes three levels of analysis that represent three different scales of movement with movement steps as the highest resolution, followed by movement phase, and lifetime tracks. Seidel et al. (2018) reviewed multiple movement parameters which were ordered by different scales of analysis. They especially classify movement parameters as trajectory related or space use related. Based on this work, to analyse the movement of



(a) movement paradigm

(b) levels of analysis

Figure 1.1 – (**a**) The general movement paradigm of Nathan et al. (2008). (**b**) The following three levels of analysis were derived from the above described theories. These levels are used to navigate through the analysis executed in this thesis. Every level comes with its assumptions, uncertainties about data quality and scales, and the corresponding effects (Laube, 2014). But the general movement paradigm stays the same (Nathan et al., 2008).

orangutans, I propose the following levels of analysis: 1) The highest spatio-temporal resolution relates to movement of minutes to hours. Possible behaviours to research on this level are, e.g., the pattern of active avoidance or a directed movement between food sources. 2) On the level of intermediate resolution, we have a spatio-temporal resolution of one day, which is very distinct for orangutans with their diurnal behaviour and is therefore widely used as a standardised level of analysis for analysing e.g. DJL or energy intake per day (Seidel et al., 2018; Vogel et al., 2017). 3) On the lowest resolution level, we find the space use patterns which are analysed by using home range models and core range models and various algorithms used to derive them (Seidel et al., 2018).In previous studies, the timescale of analysis varied a lot. Often the timescale was adjusted to the dataset or the research question. If enough data was available and e.g. the age-sex differences were analysed, home ranges were e.g. calculated every year (Ashbury et al., 2020). If less data was available home ranges were calculated over the whole research period (Singleton and Van Schaik, 2001). Up to now, not much is known as to how such differences in time scales alter the results obtained in the analyses conducted.

1.6 Orangutan behaviour and spatial characteristics

Figure 1.2 – Photography of female orangutan Lisa and her offspring Lois (*Pongo abelii*) by Maxime Aliaga.

There are three different orangutan species. One of them lives in the Malayan and Indonesian part of Borneo (*Pongo pygmaeus*) and two on Sumatra, Indonesia (*Pongo abelii and pongo tapanuliensis*).The *Pongo tapanuliensis* species was just recently described as a new species, Nater et al. (2017). There are multiple orangutan study sites, (see Wich et al., 2009, xxii) and the web page of the University of Zurich Orangutan-Network (2021) for an overview.

As a cognitively advanced animal, orangutans show a wide range of behaviours and rely on locally bound knowledge. Males disperse from their natal area to a breeding site, which is what we expect, promotes knowledge transfer between areas (Setia et al., 2009b; Singleton et al., 2009). Orangutans are large bodied, semi-solitary, mostly arboreal and frugivore mammals. Their social community is best described as a loose neighbourhood where the nearer the better the individuals know each other and no spatial nor social exclusivity is claimed (Galdikas, 1982; MacKinnon, 1974; Setia et al., 2009b; Singleton and van Schaik, 2002).

Orangutans show sexual dimorphism and there are five main age-sex classes, which differ in various behaviours. Upon reaching sexual maturity at the age of 15, orangutan males leave the area where they were born. Adult, sexually active males then undergo another phase called unflanged stadium where they resemble females and travel far between areas. The clear mechanism when and why males enter the flanged male stadium is not yet fully understood. It is hypothesised that developing into a flanged male may be worse than arrest in the unflanged male stadium when their is the risk of not being the main dominant flanged male for an area based on other more dominant flanged males. The more mobile unflanged males have the advantage of actively searching for females and initiate mating. Females tend to resist mating attempts or matings occur during phases of low chance of fertilisation. They prefer the dominant flanged male of a region which is mostly found by its distinctive long calls where the dominant flanged male often has long consortships in which they almost fully control the mating access to the estrous females (Atmoko et al., 2009; Dunkel et al., 2013).

Females are philopatric (see above) and therefore clusters of related females occur (Ashbury et al., 2020; Knott et al., 2008; Morrogh-Bernard, 2009; Nater et al., 2017; van Noordwijk et al., 2012). During their developmental process they start travelling more when becoming sexually active with the age of around 15. During this exploration phase they tend to have bigger home ranges before settling near the mother's home range Ashbury (2013). Adult females are normally accompanied by one dependent offspring (i.e., infants) and sometimes also by a semi-independent offspring (juvenile or independent immatures see Glossary for age-sex classes). Offspring are weaned at the age of eight years in Suaq (van Noordwijk et al., 2018). While infants are in constant association with their mothers, independent immatures may already explore the environment by themselves and move independently. The main social units in orangutan populations are therefore single adult males (flanged or unflanged), mothers with one or two dependant offspring, and independent immatures (old categories: sub-adult or adolescent females and males) (Galdikas, 1982; Van Schaik, 1999). Gatherings of orangutans, which are called parties, are observed frequently where party sizes are bigger on Sumatra than on Borneo. Parties are assumed to be strongly influenced by food availability. But for Suaq, no systematic temporal change in party sizes has been observed, which is possibly due to high and stable food availability (Morrogh-Bernard et al., 2009). Thus active avoidance due to male-male competition but also due to scramble competition between females occur. Unflanged males (which have larger ranges) tend to avoid regions of flanged dominant males (which have smaller ranges) (Singleton and van Schaik, 2002). For maintaining distance between other individuals flanged males often use so-called long calls (Atmoko et al., 2009). But active avoidance is also described between females, although females do not use long calls. The female scramble competition has been described as much more subtle, with few encounters. Passive range exclusion was argued to be one of the mechanisms how passive range exclusion happens but this theory assumes a higher food availability between core range overlaps than within core regions (Stewart et al., 1997). Therefore individuals establish home ranges where the are less forced to travel deeo into other individuals home ranges. However, if female agnostic interactions (fights) occur, females within their core ranges win predominantly (Knott et al., 2008). Relatedness additionally showed to explain less avoidance between individuals for Tuanan (van Noordwijk et al., 2012). Orangutan population densities, which are highest in Suaq, have been shown to be influenced by the quality and availability of food (Husson et al., 2009). Orangutans generally spend a lot of effort and time to reach sufficient energy intake. They spend around 50% of their activity time feeding, where fruits are the main food source (62.7–69.6%); others are bark (0.8–1.4%), invertebrates (14.6–12.2%), leaves (18.3–12.7%), flowers and rarely even slow loris (*Nycticebus coucang*) and other small mammals (Hardus et al., 2012; Morrogh-Bernard et al., 2009). On Sumatra, fruit is eaten more often and is more readily available, whereas on Borneo, bark and leaves are eaten more when fruit is scarce. In peat swamp forests, bark is eaten more often and forest type matters explaining the consumption behaviour (Morrogh-Bernard et al., 2009). Among the three orangutan species, *Pongo abelii* have the largest brains, the slowest life history, and are the most gregarious.

Generally, two strategies of orangutan feeding behaviour are described. A "sit and wait" strategy in forests where food availability is irregular (e.g. in Gunung Palung) and a "search and fin" strategy where food availability is regular (e.g., in peat swamp forests in Suaq and Sabangau) (Morrogh-Bernard et al., 2009). In Tuanan, Wartmann (2008) found a slight trend of differences in movement speeds, TDD and DJL between higher and lower FAI, but the variation between individuals tended to be bigger than between different fruit availability periods.

Until now, there was only one distinct main difference found between the positional behaviour of orangutans on Sumatra and the ones on Borneo (Luskin et al., 2017). Bornean orangutans tend to stay much longer periods on the ground than their Sumatran counterparts, which are almost exclusively arboreal (Ashbury, 2020). According to Cant (1987) this may result from the lack of big predators on Borneo, in contrast to Sumatra with its sympatric living Sumatran tigers (*Panthera tigris sumatrae*), although Sumatran tigers are on the brink of extinction nowadays (Luskin et al., 2017). Generally, all orangutan species are arboreal and their low extrinsic mortality may relate to this, for instance because of a lower exposure to predators, humans, and human borne and other diseases (Ashbury, 2020; Woodford et al., 2002).

Although some studies looked at orangutan range use and movement behaviour, only very little is known about the whole picture of the spatial representation, including, for example, to what extent external factors influence space use or how much various individual factors influence space use because the underlying factors have to be further analysed and the scales and methods of analysis have to be compared (Figure 1.1a). In summary: the species, populations, age-sex classes and the surrounding habitat play a key role in explaining the spatial behaviour of orangutans. An important approach for orangutan studies is to compare the different study sites within and between the species and habitats. Doing more confirmatory studies of already existing results, for example, by comparing new data sets collected with GPS devices with older studies of hand-drawn orangutan locations, additionally adds significance. This Master thesis aims to do this by comparing the results obtained in Suaq to results obtained from the Tuanan study site in Borneo, which has a good data coverage and a history of several studies about movement indicators that were conducted there.

There is a general guideline for orangutan field research, which allows to compare the data between sites. Unfortunately, there is to this day no central storage or standardised database for the collected data sets. Comparative studies between sites and between earlier studies (before 2000) are therefore impeded. The data collection at various research locations is normally executed by trained staff conducting focal animal follows. A focal refers to the orangutan which is being observed. A special hominoid behaviour is useful for normalising these focal animal follows: nest building. Nest building is rare in the primate order but the great apes, including the orangutans construct nests from tree twigs and leaves. They are mostly used as sleeping places in the evening but sometimes for other occasions, such as for resting during the day Prasetyo et al. (2009). For spatial analyses, this is a useful behavioural trait because the focal animal follows normally start at a morning nest and end at a night nest, reflecting the diurnal orangutan behaviour. From an analytical point of view, such nest-to-nest (NN)-follows can be seen as a standardisation of movement over a day. Older spatial studies of orangutans are normally based either on undigitised or digitised hand-drawn locations on a map of such NN-follows, whereas newer studies from 2000 onwards use handheld GPS devices, which are later combined with the behavioural information gathered simultaneously.

1.7 Research questions and hypotheses

The following questions are focusing on orangutan movement in Suaq:

They aim to disentangle environmental and social effects on movement parameters of Sumatran orangutans and compare them to the comparison site in Tuanan.

RQ A.1 *What characterises orangutan movement (see 1.5)? and on which levels do we have the chance to analyse it with the available data (see 1.5)? Are basic movement parameters in accord with the literature and specifically with the previously analysed data set of Suaq from before the 2000s in Singleton and Van Schaik (2001) (see 3.3) ?*

Orangutan movement is expected to be slow with a low amount of quick movement or strong dynamic changes compared to other primates. The movement is expected to be unimpeded by the environment. Additionally, I expect that the temporal resolution allows us to see nearly every nuance of movement, although brief movements, e.g, during competition or flight may be out of reach. A type of instantaneous avoiding patterns as the highest possible resolution limit may be observed. I also expect to be in accord with the previous data analysis where they found average DJL of 830 m for adult females and validate previous findings by Singleton and Van Schaik (2001) DJL (Section 1.1).

RQ A.2 *Can these daily movement parameters give useful insights into spatial behaviour (see 3.3.2)?*
The DJL is expected to be a representative indicator of the travelled distance in reality because a sampling interval of 30 minutes detects most of the common rather slow movement behaviour of orangutans. Accordingly, the tortuosity is expected to detect more directional or indirect movement, although the effects may not be as telling due to multiple effects and assumptions. For example, Benhamou (2004) states that the SI is useful to describe the efficiency of a walk from A to B but not so much to describe a random search path. Therefore, the sinuosity index as a more advanced tortuosity measurement was calculated as well.

RQ A.3 *How are daily movement parameters influenced by external and internal factors such as weather, fruit availability, age classes and offspring age (see 3.2)? and what are the differences between Suaq and Tuanan (see 3.3.3)?*
It is expected that age classes play a significant role in explaining DJL and SI, where the former is expected to be higher in independent immatures, nulliparous/adult females and unflanged males, and the latter to be higher in infants and independent immatures, which are expected to plan their routes less efficiently and to test their locomotion techniques more randomly (Alavi, 2018; Chappell et al., 2015; Schuppli et al., 2016). Fruit availability is expected to play a much weaker role than in Tuanan because Suaq is one of the most productive orangutan habitats and therefore even in periods of low fruit availability it is higher than at most other research sites. In Tuanan and even even Sumatran sites like Ketambe FAI explains a lot of variation in DJL Morrogh-Bernard et al. (2009); Wartmann (2008). Although Wartmann (2008) showed that the tortuosity of movement did not change with altering FAI.
Weather variables are expected to play an important role for the timing of the start and end of activity but their impact on the whole DJL or SI is unknown. I predict that especially precipitation affects DJL negatively due to observations of later activity start, and many behaviours showed during rainy weather such as rain-hat construction, roof building (against sun or rain), bunk nests (resting under newly constructed or old nest) and shelter seeking under nests or even on the ground (MacKinnon, 1974; Van Noordwijk et al., 2009). If weather

variables do affect the daily travel distances or movement patterns, it is expected that such external factors do influence all age-sex classes equally. A more pronounced search-and-find strategy is expected in Suaq and therefore fewer variation and higher values for DJL are expected compared to Tuanan (Morrogh-Bernard et al., 2009; Wartmann, 2008). Flanged males and unflanged males DJL are expected to differ similarly as in Tuanan but due to more stable dominance hierarchies in Suaq and therefore less confrontations between males they are expected to be more different from each other, with clearly lower values for flanged males than unflanged males (Hayward, 2018). Flanged males are therefore expected to travel less far than in Tuanan because their movement is mainly a response to mating strategies. The more stable dominance hierarchies do not require to travel further. Although overall we expect longer DJL for Suaq compared to Tuanan because of the higher FAI. Age categories are expected to influence DJL positively and SI negatively because younger individuals are expected to struggle more to plan their daily routes (Schuppli et al., 2016). But due to different age phases where especially young females travel much more the youngest age categories for adult females show higher DJL Ashbury et al. (2020). Offspring age is clearly expected to positively correlate with DJL but to show no effect in the SI similarly to Tuanan (Wartmann, 2008).

The following questions are focusing on female ranging behaviour only:

They aim to compare home ranges and ranging parameters of resident females of Sumatran orangutans to the comparison site in Tuanan, which differs in food availability and sociability.

RQ B.1 *How big are home ranges and core ranges in the high orangutan density habitat of Suaq (see 4.2.4), and which factors influence the home range itself (see 4.2.5)?*

Singleton and Van Schaik (2001) found home range sizes of 8.5 km^2 using MCP for female orangutans in Suaq, which is bigger than what other studies found (Ashbury, 2020; Knott et al., 2008; Singleton et al., 2009; Wartmann, 2008). These big home ranges were explained by the patchiness of food sources. The results of my analyses are expected to be in accord with the findings of Singleton and Van Schaik (2001) especially for MCP results. Potentially my results are a bit smaller due to the exclusion of outliers (95%). The high number of feeding trees is expected to reduce home range size. Similarly as described in Tuanan for lower fruit availability periods (Wartmann, 2008) core ranges are a third the size of the 95% home range for Tuanan. A more pronounced "search-and-find“ strategy, and the higher population density are possible explanations. Because passive range exclusion may be more pronounced in Suaq due to the higher population density, which leads to higher avoidance even in core areas and therefore relatively bigger core areas. To test if passive range exclusion even is a model for Suaq insights are added from the analysis of fruit trees in the core range or full home range and the overlaps. If there is passive range exclusion, fruit trees are expected to be more abundant in overlaps than in core regions. Therefore it is not worth fighting over core regions (Knott et al., 2008; Stewart et al., 1997).

RQ B.2 *What differences can be observed between different home range algorithms (see 4.2.3)?*

There are more precise methods than MCPs nowadays for measuring home range sizes as so stated in Wartmann (2008). Newer algorithms, such as KDE, should be more expressive. The two algorithms, Biased Random Bridge (BRB),Autocorrelated Kernel Density Estimation (AKDE) which include even a temporal dimension for extracting a home range, are expected to describe observed patterns, such as the influence of fruit trees even better than KDE. I expect MCP to find the biggest home range sizes followed by KDE. The BRB algorithm is expected to slightly smaller due to the inclusion of time. Thre results of the AKDE algorithm are difficult to predict but I assume similar sizes as for BRB if we have enough samples.

RQ B.3 *How big are home range overlaps in Suaq (see 4.2.6), and does the matriline, dominance, age category, and amount of fruit trees explain the relative sizes of overlap (see 4.2.7)?*

The home range overlap, seen as a proxy for tolerance of sharing the own range, and its resources are expected to be bigger between near relatives, and therefore the relatedness of orangutans to have a positive effect on the overlaps. Female philopatry intensifies this by near home range establishment of offspring (Ashbury et al., 2020; van Noordwijk et al., 2012). Therefore, relatedness should positively influence relative overlap. The dominance difference between orangutans is expected to be negatively correlated with overlap size because dominant females are able to exclude less dominant females from their range. The effect of age on overlaps is unclear, but probably similar age does increase sociability and therefore increase overlaps. To analyse overlaps also a normalised fruit tree value will be analysed. They are expected to confirm that fruit trees may be shared more between related females and that higher dominance ranks lead to less number of normalised fruit trees in overlaps.

Chapter 2

General methodology and data preparation

This Chapter presents the general methodology employed for data preparation. In Section 2.1 the methods for data gathering, pre-processing and processing are described. In Section 2.2 first results from these preparatory steps are shown and discussed.

2.1 Data processing

2.1.1 Study area

The study area of Suaq Balimbing (3° 42' N, 97° 26' E, approx. 75 m a.s.l.) lies on the western coast of the Indonesian island of Sumatra in the politically and naturally troubled area of Aceh (Figure 2.1). Studies on the orangutans in Suaq started as early as 1992. After political unrest in Aceh, the research station was closed in 1999. In the aftermath of the disastrous Tsunami of 2004, peace efforts between the central government of Indonesia and the province of Aceh were successful and allowed the resumption of research in 2007 (Crisis Management Initiative, 2005; Wich et al., 2009).

The research station with its small and simple houses is located directly at a small river. The river was not a barrier for orangutans before some degree of forest clearance happened on the western side (Singleton and Van Schaik, 2001). The station represents the entrance to the mostly flat riverine peat swamp forest on the other side of the river where the study area is located (Figure 2.5). The forest is largely undisturbed and the density of large trees is higher compared to the disturbed peat swamp forest in Tuanan (Wartmann, 2008). Large trees showed to be used more often for moving through the canopy than expected (Manduell et al., 2012). The trail system representing a research grid is composed of narrow trails that are maintained and on one trail there is a narrow boardwalk, made of of wooden boards. The terrain altitude in the study area is nearly sea level. The soil is muddy and many back swamps are regularly underwater; therefore, the forest structure is irregular. The water level is regularly measured at the river near the station. The flat peat swamp forest extends further out of the study area to the north up to where the hills and mountains of the Leuser Range start to ascend. The east is bordering to smaller hills and in the south to further peat swamp forest all the way to the seashore, which is located approximately 10km to the southwest. Surrounding hills consist of mixed dipterocarp forest.

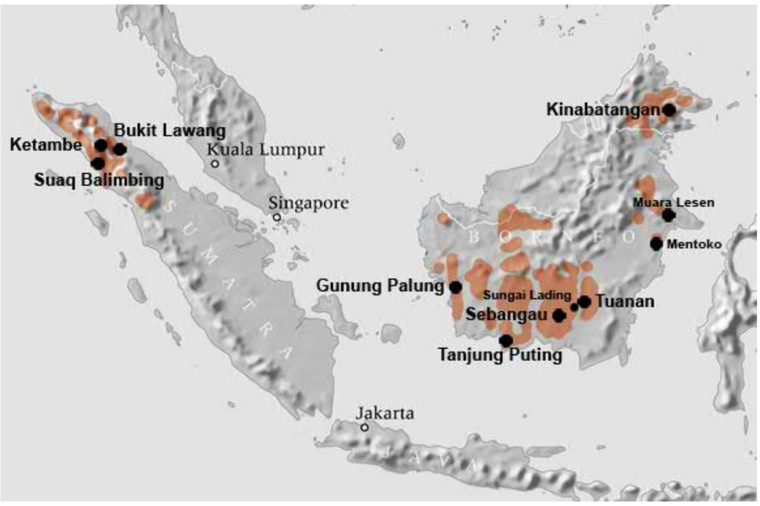


Figure 2.1 – Most research sites for orangutan studies available on the web page of the orangutan-network (Orangutan-Network, 2021).

2.1.2 Data gathering, pre-processing and processing

An overview of the whole data workflow can be seen in figure 2.2. The following procedure is derived from the standardised field methods for orangutan research (Orangutan-Network, 2021). In earlier times of the research in Suaq mainly one follow was executed per day. More recently additional assistants and more efficient processes allowed multiple follows per day. For finding an orangutan an opportunistic approach is used. On most search days, the first

orangutan which is encountered during searches starting at the research station will be followed. Infants or independent immatures who accompanied their mother were noted if the mother was followed as well as the other way around. To access the study area, the trail system is used. The position of the night nest is used to find an orangutan to follow the next day. Thus, focal selection may be influenced by the location of the research station and by the follows of the previous days. To minimise the researchers' disturbances, orangutans are maximally followed ten days in a row and accordingly the temporal correlation of follow selection is minimised (Schuppli, personal communication 2021).
Follows ideally start at a morning nest and end at night nest. Sometimes the focal individuals are found already outside of the nest or are lost during the follow which is marked as different GPS point types. The activity of an orangutan is written down every 2 minutes, whereas a GPS location is taken every 30 minutes (e.g., at 7:30 am). To measure the orangutan's location the orthogonal point below the orangutan is taken while keeping the positional Dilution of Precision (DOP) displayed below 12 m. Mostly positional error values lie below 6 m (Schuppli, personal communication). The location is mostly measured after the focal orangutan left the location to minimise impact on the animal (e.g., at 7:43 for the position noted at 7:30). The GPS used devices are Garmin models GPSMAP 62s, GPSMAP 64s, and GPSMAP 78 (Schuppli 2016). Additional GPS points are taken, at every nest (morning-, day-, night nest) or at the start and the end of a focal follow. Other occasions where GPS points are taken are, for example, when another orangutan comes closer than 50 m, which is called a party, when a long call is given or heard, when an orangutan is found but not followed, when an orangutan is in a feeding tree for more than 5 minutes, when tool use occurs, or when DNA samples are taken.

Weather parameters are measured twice each day at the research station. In the morning and the evening, the temperature maxima and minima, the precipitation in mm, and the river's water level are measured. Furthermore, every month an assessment of the fruit availability in Suaq is done by calculating the number of fruiting trees in relation to a total of feeding trees. The assessment is based on two phenology plots containing over 1000 trees that go from north to south and from east to west.

For further data analysis, only the spatial data was used since the focus of this work was

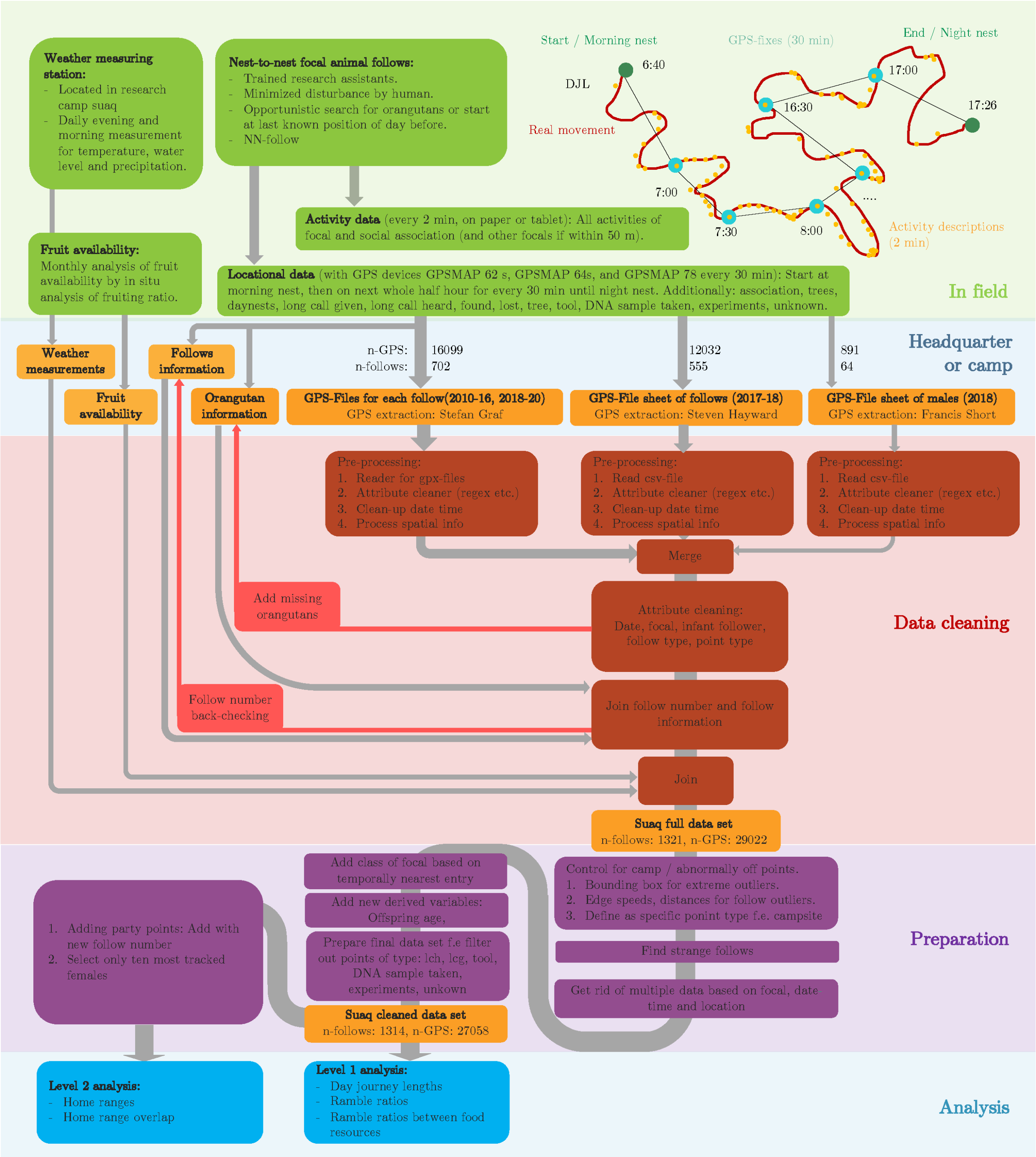


Figure 2.2 – Overview of the workflow from data gathering, pre-processing, processing to the final data analysis. **Point types:** Every GPS point is assigned a label for its type, with possibilities: range or so-called 30-minutes point, morning nest, day nest, night nest, party, long call given, long call heard, found, lost, tree, tool, DNA sample taken, experiments, unknown (additionally introduced point types just for data processing purposes are: potentially campsite, abnormal off point, party2). **Follow types:** Nest-to-nest (NN), found-to-lost (FL), found-to-night nest (FN), morning nest-to-lost (NL). **Follow numbering:** Regular follow numbers are from 1 to 2949 (last follow included 29.02.2020); if no follow number was registered in the follow sheet (e.g., possible single observation), numbers are from 1000001 to 1000019 (new follow numbers given, starting with 1000000); if error follow number 9999 was given by Steven Hayward for multiple follows with no follow registered, follow numbers are from 1100001 to 1101351 (new follow numbers given stating with 1100000); if GPS points of type party were added as new follows, numbers are from 1110001 to 1110095 (new follow numbers given starting with 1110000).

on the analysis of individuals' space use rather than their activities. After collecting activity and spatial data in field, the follow number and specifics are derived when back in the camp, which generates another data set of follow specifications.

As a starting point for this thesis, seven data sets were available. Three data sets of the GPS data for Suaq. Three, because different studies already cleaned parts of the data for different purposes, for example, for specific years by Hayward (2018) or for specific sex classes by Short et al. (2020). The other four data sets were the fruit availability and weather measurements, the follow specifications, and finally a list with informations about the orangutans, such as their name, estimated birth date, matriline, and sex, along with others. All GPS datasets were reprojected from the *WGS84* (EPSG: 4326) coordinate system to the local national spheroid *DGN95 / UTM zone 47N* (EPSG: 23867) with Cartesian coordinates. Furthermore, the dates and times were cleaned and the timezone was defined as Asia/Pontianak (UTC+7), albeit sometimes some packages override the time zones to UTC for simplicity. After combining all GPS data sets the follow specifications were added if possible. Inconsistencies were corrected either in the follow data set or in the spatial data set. Afterwards, further variables, such as the orangutan information, weather, and FAI information were joined. The age was derived from the estimated birth date to the date of follow, whereas the offspring age was calculated by the offspring birth date to the date of the follow. Infants were defined as maximally seven years old, which is the lower threshold of the weaning age in Suaq (Van Noordwijk et al., 2009). For offspring age, only the youngest infant was considered for the analysis; multiple infants only occurred in 8 follows, when using a weaning age of seven years.

After having obtained a full spatial data set, the follows were again cleaned based on spatial properties, including outliers, whereby data was deleted very conservatively and only on clear criteria. Deletions were either visually accessed and then deleted or points were just marked as outliers. E.g. were many points near the research station marked as outliers. For the analysis of movement patterns, subsequent point types were excluded: long calls given and heard, DNA sample taken, experiments, unknown, potentially campsite, abnormal off point. For the analysis of home ranges, the same points were excluded, but additional locations were generated by using party points as a location for the dependant orangutan.

2.1.3 Hardware and Software

For all preprocessing, processing to analysis and visualisation, the *R* (4.0.5) programming language was used using the *RStudio* (1.4.1106) integrated development environment (IDE) (R Core Team, 2021). A Macintosh machine (OS X 10.16.0) with an eight-core M1 processor and 16 GB of memory was used. Table 2.1 lists the scripts and packages used in preprocessing (PP), analysis of daily movement (MA) and analysis of home ranges (HA), except some additional scripts used for exploratory analysis. The full R code scripts are available in my own GitHub repository (`https://github.com/greentrea/SUAQr` Graf 2021). Results such as home ranges or day journey lengths are not available but can be provided on request in agreement with the data manager (Dr. Caroline Schuppli).

Table 2.1 – Overview of important R packages used.

R package	version	usage	purpose	year citation
lubridate	1.7.10	PP, MA, HA	handling times and dates	2021
dplyr	1.0.5	PP, MA, HA	data wrangling	2021
tidyr	1.1.3	PP, MA, HA	data wrangling	2021
tidyverse	1.3.0	PP, MA, HA	data wrangling	2019
stringr	1.4.0	PP, MA, HA	extracting strings, regex	2019
sf	0.9-8	PP, MA, HA	import, geometric operation	2021
rgdal	1.5-23	PP, MA, HA	handling spatial reference systems	2021
RColorBrewer	1.1-2	PP, MA, HA	handling color visualisation	2014
trajr	1.4.0	MA	trajectories, interpolating, straightness	2020
adehabitatHR	0.4.19	PP, HA	HR calculation, Schoeners I	2006b
ks	1.12.0	HA	KDE bandwidth calculation	2021
move	4.0.6	PP, MA, HA	move objects for ctmm analysis	2020
caTools	1.18.2	HA	quality of home ranges	2021
ggplot2	3.3.3	PP, MA, HA	plots	2016
gridExtra	2.3	PP, MA, HA	plots ordering	2017
GGally	2.1.1	MA, HA	overview scatterplots	2021
ggfortify	0.4.11	MA, MA, HA	diagnostics	2016
lme4	1.1-26	PP, MA, HA	generalized linear mixed effects	2015
lmerTest	3.1-3	MA, HA	p-values of linear mixed models	2017b

PP: preprocessing and processing, MA: movement analysis, HA: home range analysis

2.1.4 Statistical analysis

As a first step, an overview was gained by using the GGally package and its ggpairs function, which uses scatterplots and the Pearson's correlation coefficient to give an overview of the data.

To investigate the effect of the explanatory variables explaining DJL, SI, home range size and home range overlap, linear mixed effect models (LMM) with a Gaussian error structure and identity link function (implemented in the lme4 package 1.1-26) were used. Linear Mixed Models have been used increasingly in the field of of ecology and evolution biology (Bolker et al., 2009; Harrison et al., 2018). They extend traditional linear regression models by including a fixed and a random part of the explanatory variables. The usage of random effects in movement ecology is very useful. In many cases the data included lot of noise and response variables were affected by factors that are outside the scope of this thesis. The possibility of correcting for these effects is one of the main advantages. Ecological data sets are mostly very complex data sets. Often they are biased, clustered and non-independent (Harrison et al., 2018). The introduction of a random effect can correct for such non-independence. LMMs also do not require normally distributed data.

All the spatial parameters in the Analysis I and in Analysis II of this work were used as response variables, while external factors (weather, FAI) and internal factors (age, age of offspring, age-sex class, matriline) were used as predictor variables. Possible random effects were date, the focal or the age-sex classes (Section 3.1.3), whereas for home ranges they were the focal individual, the algorithm used, or the research period. The models were fitted via REML or maximum likelihood, implemented in the lmer() function of the lme4 package. To examine potential collinearity between explanatory variables the Variance Inflation Factor (VIF) of the fitted models using the vif.mer() function of the lme4 package was calculated. If the VIF is below 3.0, collinearity is considered as not a problem (Zuur et al., 2009). If high collinearity was detected among explanatory variables (i.e., VIF ≥ 3.0), the ones which explained the most avriation of the colinear factors were kept until the VIF was below 3.0 (this was especially the case for weather variables). The assumptions of homogeneous and normally distributed residuals were checked by plotting the residuals against the fitted values. In order to establish if our models with predictor variables are able to explain the dependant movement variables better than a random model, the fitted models were compared to the respective null model with only the random effects. Using a likelihood ratio test implemented in the anova() function we could either accept or reject that we found a model which explains the movement patterns better than the null model, respectively. To compare different models with different numbers of predictors the anova() function was again used which gives us again the log likelyhood but also further information criteria such as the Akaike information criterion (AIC), Bayesian information criterion (BIC), which were also used to access the quality of a model (Neath and Cavanaugh, 2012; Sakamoto et al., 1986). To obtain p-values for the different explanatory variables the lmerTest package was used, which calculates p-values using Scatterthwaite's degree of freedom method (Kuznetsova et al., 2017a). The models were defined beforehand and not optimised during the process to prevent coincidentally fitting a model to the data. The aim was to find potential relationships where we then could further investigate how good an optimised model could explain the response variables. Diagnostic plots were checked by using the ggfortify package or the available functions of lme4. Finally, the models were fitted and analysed. The Linear Mixed Model (LMM) models were only adjusted if there was a problem with the variables, for instance, if some weather variables had to be removed due to high collinearity between the different weather variables.

2.2 First overview

In the following, an overview of some of the characteristics of the processed data sets will be presented and discussed.

2.2.1 Orangutan spatial data

Who was when sampled?

The number of follows and the amount of data vary substantially over time (Section 2.2.1). The spatial data for Suaq is heavily unbalanced in terms of sampling effort per individual and age-sex class. For the females we can see that the three main females tracked are responsible for nearly 60 % of the data of females (male: n = 543; female: n = 771) (Figure 2.3). This has to do with the main study goal of the research station, which is more focusing on qualitative and behavioural analysis. The location of the research area and the site fidelity of orangutans further explains the focus on a limited number of individuals.

The study duration reflected in the data used in this thesis was 9 years and 163 days, where the first follows were conducted in 2010 and the last sampled follows are from 2020, but the main study is still ongoing. Roughly four research periods can be identified, where the first period is from before 2012, the second one is from 2012 until 2016, the third one from 2016 until August 2018, and the last one starting from 2019 onward. Ashbury et al. (2020) showed that home range size and location change in young females who are establishing their home ranges. It can be assumed that slight to medium shifts in home ranges can occur over the study period of 10 years. Therefore, these research periods are used as an instrument to notice such patterns of home range shift or expansion phases.

The mean follow duration was 12:01:47 hours (Q1 = 11:32:00, Q3 = 12:40:00, n = 640), for nest-to-nest follows. For NL follows the average was 7:55:09 hours (n = 115), for FN follows 6:45:20 hours (n = 349), and for FL follows 6:08:13 hours (n = 62). A one way ANOVA of NN-follow duration indicates no difference between different age-sex classes and their overall mean (F(4,626) = 0.251, p = .909) and we can see all of them having almost the same activity or observation duration distribution from nest-to-nest (Figures A.1 and A.2).

First looking at the number of different follows per class, we see that approximately half of the follows are of type NN and another third is of type FN. This reflects the opportunistic follow scheme, where if another orangutan is found on the way it will be followed as well if the team of observers is big enough. Furthermore, around 115 follows end by losing the focal orangutan. Comparing these with the number of successful NN-follows, we can estimate a success rate of around 85% of not losing the animal on the way, assuming all NL follows were aimed to be NN follows and not an additional orangutan which had lower priority like many of the FL follows.

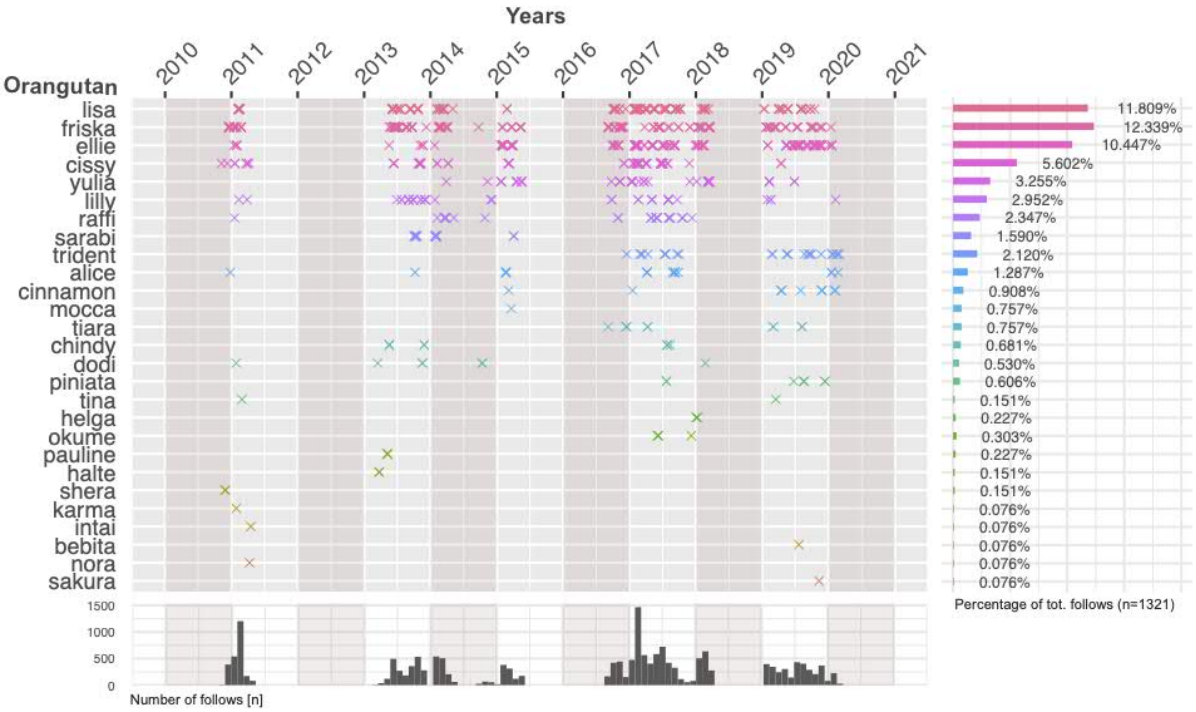


Figure 2.3 – Visualisation of the data set of female orangutans after data processing. Sown are all conducted follows over time for each female orangutan. On the right, the percentage relative to the whole data set for every female orangutan is given. Female orangutans accounted for 59 % of the data. The bottom panel depicts the histogram of the number of GPS Points collected over time, where one bar equals a duration of three months. The ordering of individuals in the list corresponds to the total number of GPS points collected. Lisa has the most number of GPS points recorded but is second only in the number of follows.

Sampling harmonisation necessary?

Irregular sampling intervals can influence the analysis of movement on Level 2 by biasing the inherent underestimation of DJL and other movement parameter (Calenge, 2006a; Katajisto and Moilanen, 2006; Kranstauber et al., 2012). One way of dealing with this is to remove points to obtain equal temporal distances between GPS fixes (Zehnder et al., 2018). Of course, this process induces a loss of information. In our case this is especially difficult because sampling was executed manually. Sometimes the fixes are not adjusted to the defined sampling interval of 30 minutes and slight temporal deviations occur. Therefore, it is not possible to simply delete points until all follows and steps are meeting our harmonised sampling regime. Another way of obtaining harmonised sampling intervals consists in interpolating GPS fixes and either just interpolate missing points (called gap filling) or set a totally new sampling regime by interpolating (i.e., resampling) the whole trajectory. One problem with this is that new data points are generated, which impacts all the derived movement parameters. As an illustrative example, when points are inferred between two GPS fixes using linear interpolation, the newly interpolated points would form a straight walk, resulting in equal turning angles and SI for this segment of the trajectory. This could be similarly misleading as the original bias by missing sampled points or having unequally sampled points. A third option of harmonizing the data is known under the term burstifying or burst detection. If data is missing within a trajectory, it is split whenever this occurs. This will result in multiple splits of the original trajectories, with the advantage of equal sampling intervals per split (or burst) and no artificially added information. In our case, where we normalise movement parameters over the behaviourally defined day follows, such bursted movements are not wanted and difficult to stitch together again.

All these three methods – temporally reducing GPS fixes, interpolating GPS fixes based on trajectories, and bursting trajectories – are not useful for the presented data set. A harmonisation for analysing home ranges may be an option because also autocorrelation would be reduced (4.1.3). The advantage of such a harmonisation was weighed against the loss of information, the introduction of new biases, and the complexity of suitable resampling for our purposes. Although in our data set irregular sampling intervals do occur, the amount of irregularities is low. When including all shorter sampling intervals, which are mostly the last and first steps between morning or evening nests and the first or last 30-minutes ranging point (+35 % of all points), and including all steps with a time lag below 1 hour (+2 %) (so if one point was accidentally skipped), we already get to about 95 % of the data (Figure A.3). A last visual verification that shorter time lags do not occur more frequently during specific daytimes (e.g., because of nests and feeding trees) was done and shorter sampling intervals were found to be more or less equally distributed over the day (Figure A.5). Overall, we will compare home ranges and movement parameter results, therefore slightly unsteady sampling intervals do not seriously affect results because it is expected that all follows are similarly affected and we mainly compare results.

2.2.2 GPS accuracy

In 1998, Phillips et al. (1998) state that we have to be cautious about using GPS devices in neotropical forest and that they are probably not of practical use. The GPS devices used

(GPSMAP 62s, GPSMAP 64s, and GPSMAP 78) did not provide any DOP, which is a value for measuring the vertical, horizontal, positional and temporal accuracy of a device (Langley, 1999). The manual of the GPSMAP 62s states a horizontal positional error of < 10 m in 95 % of cases and a root mean squared error (RMSE) of ± 3–5 m (Forin-Wiart et al., 2015). The device does display an accuracy value on screen which however is not written down by the research assistant. But the data collection protocol of the site instructs researchers and research assistants to wait until the accuracy value displayed on the screen reaches a value below 12 m. Satellite availability was not mentioned as a problem in Suaq and the displayed accuracy values often dropped quickly below 6 m. The exact definition of the displayed value is expected to be a Horizontal Dilution of Precision (2D) (HDOP), which reflects the overall accuracy in 2D space (Langley, 1999). Wartmann (2008) performed a GPS accuracy analysis and found a mean positioning error of 9.8 m in Tuanan and 95 % of points were within 18 m of a predefined reference coordinate. In her analysis cloud cover, canopy cover, and time of day showed to influence the accuracy, whereas rain did not. For Suaq no error estimation has been executed until now. The analysis of handheld GPS devices and its application in movement ecology was analysed by Forin-Wiart et al. (2015). They state a similar positional error of below 10 m for handheld GPS devices. Nonetheless canopy cover, sky availability, number of satellites, and HDOP as well as the GPS fix rate (for automatic fixes logged by the research assistants' GPS device) showed to influence the actual positional error. Whereas rain and small shrub coverage do not influence the positional error of the handheld GPS device Forin-Wiart et al. (2015); Recio et al. (2011); Wartmann (2008). Based on the above literature, the analyses conducted in this thesis use a conservative GPS error estimate of 12 m where needed.

2.2.3 Researcher bias

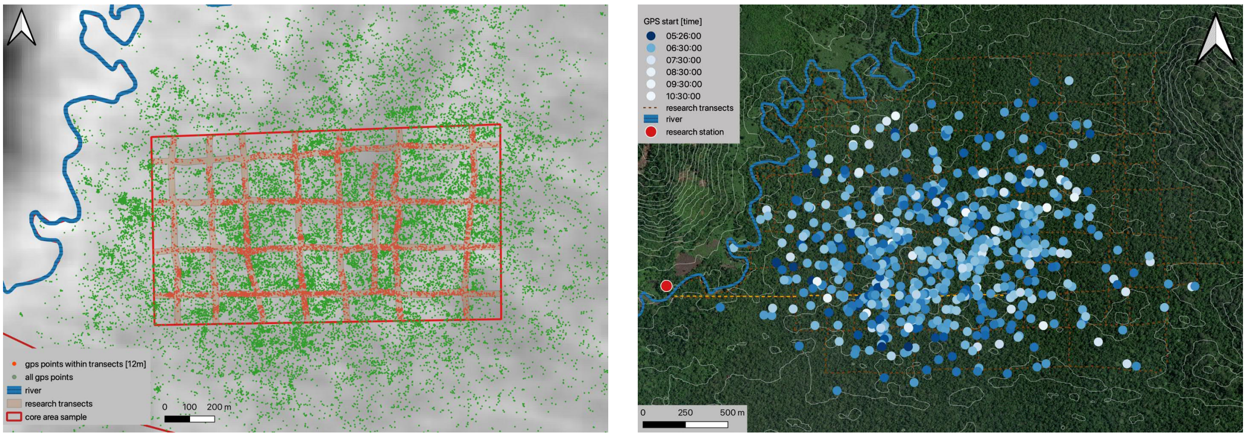
Theory and definition

Wartmann (2008), Knott et al. (2008) and Singleton and Van Schaik (2001) already pointed to biases induced by the research and following the protocol of orangutan studies relating to movement. Unfortunately, no study exists which actually quantifies these biases in detail. Singleton and Van Schaik (2001) expanded the study area temporally and stated that most originally followed females did not leave the area to the new expansion (Singleton and Van Schaik, 2001). Biases in measured GPS positions relating to the researchers and research assistants are a result of the sampling technique employed in field, for example how they are handling the GPS devices and if they are waiting to reach low DOP values. But more importantly, the spatial movement of the researcher which probably can be best explained by the study area and its established research trails (transects). Researchers and research assistants use them whenever orangutans can be observed from them but leave them if orangutans go further away. Furthermore, the research guidelines and training, the research assistants' motivation and human-orangutan interaction can influence the results of GPS positions. The literature on home range studies assumes that such influence is abundant. However, the conclusion is that there is no good solution to correct for such bias and that the influence on home range sizes — which those studies all focused on — is fairly small. Most individuals still have very distinct home ranges and especially core ranges are in usually different locations, which reflects the small influence of such positional biases. Following the individuals over a day and even consecutive days should minimise the bias originating from the research method (Knott et al., 2008; Singleton and Van Schaik, 2001; Wartmann, 2008). Nevertheless, an elevated rate of losing orangutans on the edge of the study areas is mentioned (Knott et al., 2008).

First, we have to state that such location and sampling biases always start with the finding of an orangutan. Then the starting and entry points, namely, the research station as well as the trails influence how the researchers and research assistants look for an orangutan, while they are also influenced by the previous follows of the days before and by their intuition. Even though researchers and research assistants search in the entire study area, some areas are more promising to search for and easier to reach. These areas are thus frequented more often during searches. The starting point has most likely the highest influence on the start of follows. The starts or morning nests are expected to be nearer to the research station and to the main trail system, especially to the boardwalks. Conversely, we also have to consider that the trail system may influence the locations of orangutans, when there is any change in forest structure due to the trail system, orangutans may prefer the more open forest structure, similarly to the preference of bigger trees (Manduell et al., 2012). Also, human-orangutan interaction could play a role where individual orangutans have a bias to avoid or prefer, respectively, to stay near human research assistants. However, researchers and research assistants try to minimise the interaction whenever possible by keeping a distance and remaining passive (Schuppli, personal communication).

Method, results and discussion of researcher bias

To get an impression of how such an observational bias is happening, the GPS points were analysed within R and visualised with QGIS Software (version 3.10.5-A). A visual interpretation of starting points was made for the total research area. Focusing on starting times, we see that there is no clear pattern that there are more points nearer to the research camp and that they are temporally earlier than further away from the research camp (Figure 2.4b). This is already a strong indication that starting points are not significantly biased, where it would be expected that many more starting points with earlier times are near the research station and to the entrance, than further away. On the other hand a slight stronger oversampling can be observed for the area of the main boardwalk which is located just east the same latitude as the research station. To research the bias relating the trail system a rectangular area within the highly sampled core area was analysed. This was done to compare the areas as well and see how the results differ to a uniform distribution of GPS-fixes. The trail system was buffered with a 12 m distance on both sides. First the area of the rectangle (1.06 km^2) and the area of the buffered trail system (0.26 km^2, 24% of the area) within the rectangle was calculated and compared. Second the total number of sampled GPS points within the rectangle (n-GPS = 16780) and within the buffer was counted (n-GPS = 4886, 29.1%) and compared. The same was done for starting points and ending points. First starting points (n-GPS core area = 404; n-GPS near boardwalk = 146, 36.1%) looked to be more common within the boardwalks compared to ending points (n-GPS core area = 538; n-GPS near boardwalk = 182, 33.8%). Looking at the percentages all GPS points, ending points and starting points occured more often within 12 m of the boardwalk than expected from a uniform distribution (24%). But these differences were smaller than expected. Wartmann (2008) stated 58% of starting points were within the boardwalks at the Tuanan site. In our case for the whole research area (border is not exactly defined) an only approximately 35 % of points are lying within the research transects (Table 2.2).



(a) sample rectangle area

(b) starting points and time

Figure 2.4 – **(a)** Analysis of researcher bias based on a chosen core area where the number of GPS points are compared to the number of points in the buffered research transects. **(b)** Additionally, start and end points are compared as well (Figure A.6). Visual inspection of start times show no strong spatial bias towards research station or transects. Quantitative results can be seen in Table 2.2. Elevated wooden boardwalk in orange.

The last analysis was done by comparing the density of starting points to ending points over the whole study area (Figure 2.5). The idea was to use the ending points as a proxy for unbiased density of points because the resulting points are expected to be less influenced by the research assistants' decisions and the trail system but more by the orangutans' movement. The limitation is that it is assumed that no, or only little, positional bias originates from the orangutan and that the start of the follow does not influence the end of a follow. A kernel density estimation (KDE) was executed for end points and for start points with a bandwidth of 200 m derived from the HREF method of the adehabitatHR package in R (for further information about KDE and bandwidth selection, see Section 4.1.6) and by visually inspecting different results of slightly varied bandwidth values. The resulting Utilization Distribution (UD) rasters were subtracted from each other to see areas where on average more starting points occur than expected by the assumed unbiased ending points. We found that the core area of the research site has a surplus of starting points (negative density) compared to the edges (positive density). Conversely, the areas along the edges of the study area have only a minimal surplus of ending points and a lot of more peripheral areas are nearly balanced. Therefore, there is a slight bias towards the centre and the boardwalk for starting points but no clear bias in direction of the research station. Surprisingly, there is an area in the eastern part where many more ending points occur. But such local patterns are assumed to be of behavioural origin. Comparing the areas enclosed by the 95 % contour of the utilisation distribution for end points and start points,respectively, a 20 % bigger end point area was found. But by visually inspecting the results the size difference was small and a strong outwards drift of points could not be confirmed. Finally, the points were marked where orangutans were lost during the follow. We see that in the southern region more orangutans were lost and in the eastern part many orangutans were lost at the ascent of the hills. Where there is also a hotspot of losing points at the farthermost eastern region (Figure 2.5).

We can conclude that start points are biased the most by the research transects, but ending points and the total number of GPS fixes are biased well. Presumably, some degree of bias originates from the practical problem of taking GPS fixes. It is probably easier to take a GPS point near the research transects if there is a wooden boardwalk or at least a beaten track; generally, this deviation should be acceptable. Overall, the bias is found to be much smaller than described in the work of Wartmann (2008). To get more information about the bias of the research area and data collection methods we could use nest counts from drone flights or try to follow an animal for a long period without losing it. Additionally, the vector combination for different directions of all start-to-end point vectors could give insights as to how much the outward drift in different directions of the follows would be. A quick delineation of the heat maps 95% distribution showed a slightly bigger size of the probability distribution of end points than starting points.

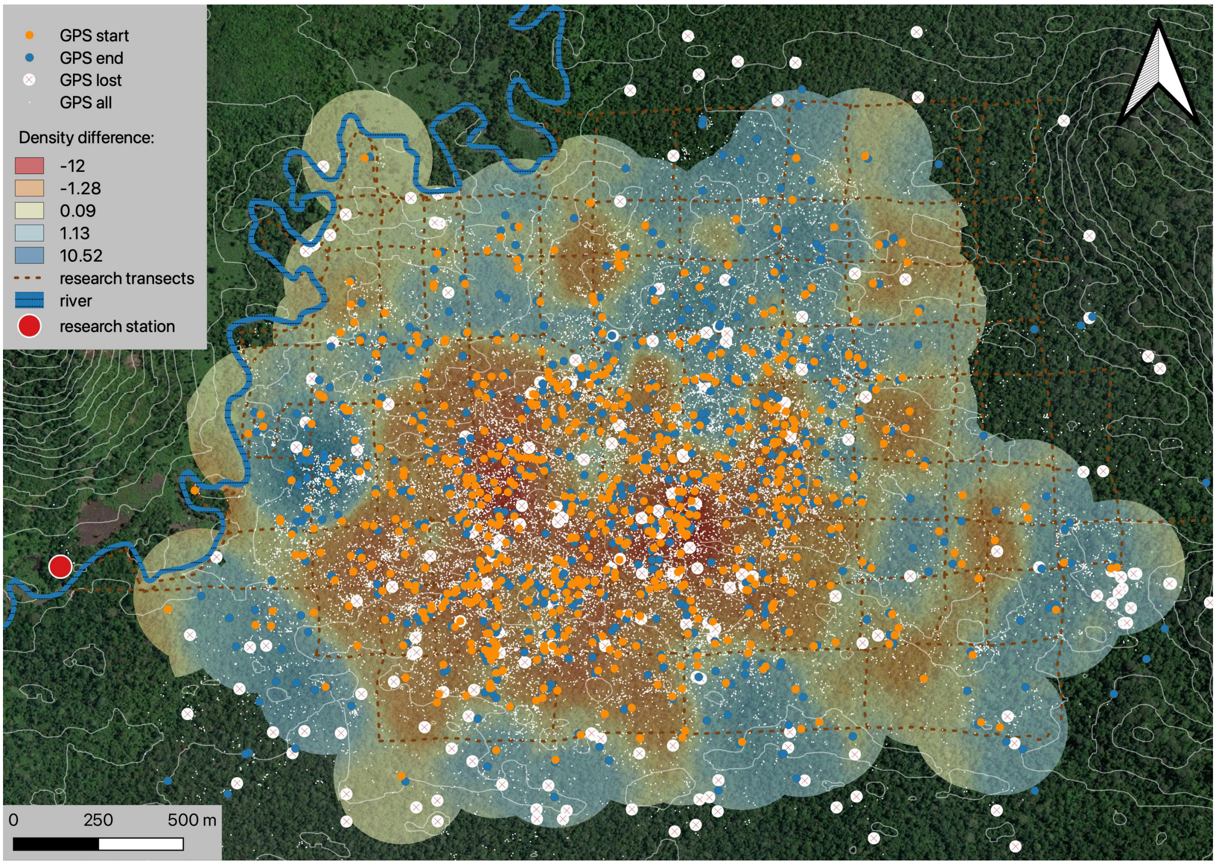


Figure 2.5 – Map of research site Suaq with contour lines and satellite imagery (ESRI world imagery): Analysis of influence of boardwalk and research transects. The research area of Suaq with its peat swamp forest in the vicinity of the Gunung Leuser National Park and close to the west Sumatran coastline. An overview of the research area with its transects and boardwalk. The elevated wooden boardwalk is on the transect line east at the same latitude as the research camp (Figure 2.4).

Table 2.2 – Analysis of influence of boardwalk and research transects. The specific core area and elevated wooden boardwalk used as a sample can be seen in Figure 2.4a.

	area	area - boardwalk	boardwalk	% of full area
area [km^2]	1.07	0.81	0.26	24.18%
n-GPS	16780.00	11894.00	4886.00	29.12%
n-start-GPS	404.00	258.00	146.00	36.14%
n-end-GPS	538.00	356.00	182.00	33.83%
tot GPS pro km^2	15718.66	14694.74	18929.47	
n-start-GPS pro km^2	378.45	318.75	565.64	
n-end-GPS pro km^2	503.97	439.83	705.11	

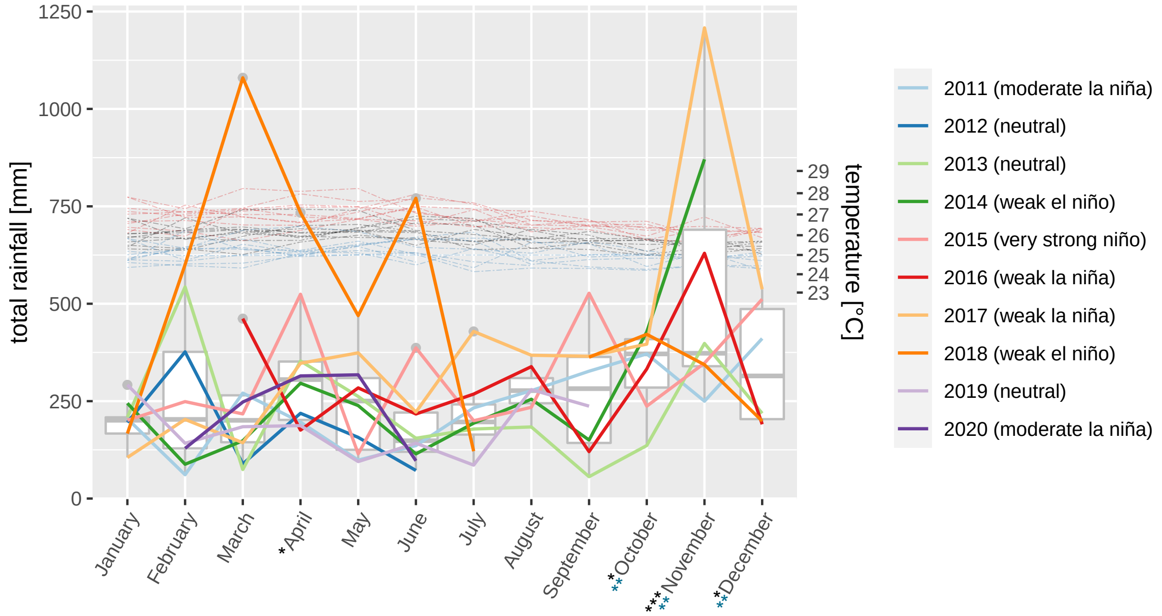
2.2.4 Weather and fruit availability

Suaq lying in a tropical rainforest region 3° north of the equator has a humid climate with greater temperature variation during the day than between seasons. Wich et al. (2009) states the amount of precipitation per year in Suaq to be 3400 mm. The data set used in this thesis resulted in very similar values but with high variations over the years (3382.4 mm ± 1113.2, n = 10) (Figure 2.6a). The minimum monthly precipitation was 56 mm and the maximum was 1208 mm. Mean monthly precipitation for all years was more pronounced for November and slightly different for April, October and December (Figure 2.6a). Clear visual and statistical differences between years were only seen for 2018. The derived mean maximum and minimum temperature as well as the total average temperature is also included in Figure 2.6. A linear regression of mean total averages of temperature with months as explanatory variables showed the months of October, November and December to be clearly different from the mean total averages of temperature. Therefore we can conclude that there is a higher rate of precipitation in the months at the end of the year which is accompanied by a very small reduction in average air temperature.

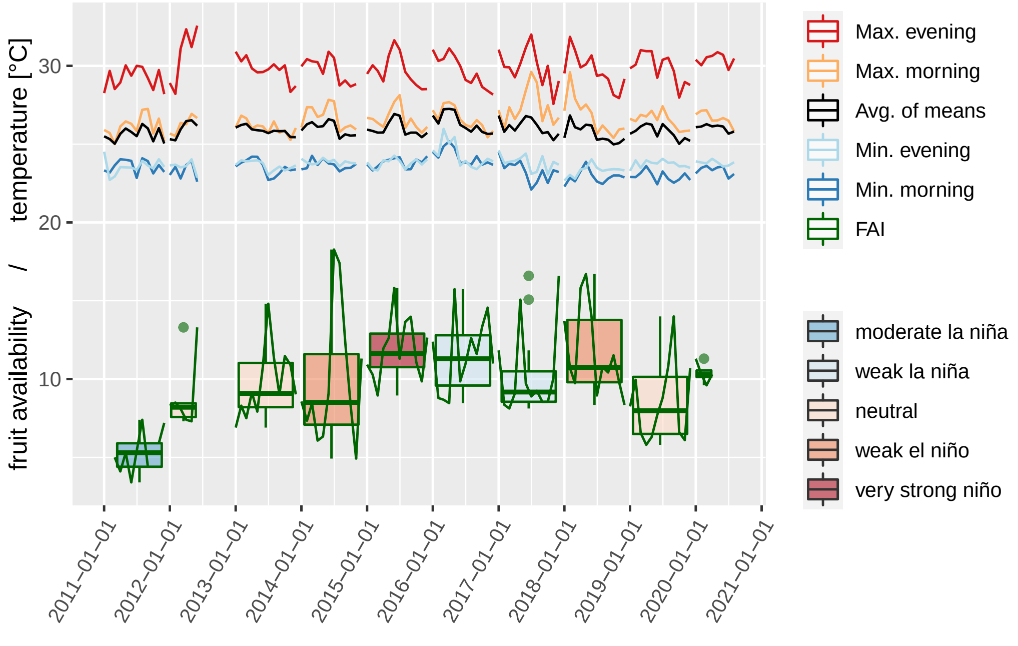
Additional information on the current state of the El Niño–Southern Oscillation (ENSO) was added by retrieving the monthly Oceanic Niño Index (SST) from the National Oceanic and Atmospheric Administration's website, which uses the data described in Rayner et al. (2003). Basically, the SST measures the difference of sea surface temperature between the eastern and the western pacific (Zones 3 and 4). A high SST value denotes a stronger El Niño and a low negative value a stronger la Niña situation (Rayner et al. (2003) for further details). This was done because many authors show an influence of the ENSO on the weather and indirectly on forest ecology and especially mast fruiting events in Borneo, discussing it as a reason for different feeding behaviours for orangutans (Russon et al., 2009; Taylor, 2009). In our case no detailed analysis was conducted. But the years were categorised by their average SST values (2.6). Additionally a quick linear regression (not included) with the SST as explanatory variable for FAI was fitted. The variance could not sufficiently be explained by the SST, but a positive influence of the SST and therefore with El Niño events was found. The same statistical analyses were also executed with another index of the state of the ENSO. The SOI, which basically compares air pressure differences on sea level between Darwin and Tahiti, was used (Ropelewski and Jones, 1987). The SOI showed a more pronounced trend in the same direction where stronger El Niño events coincided with higher FAI, but overall the total variation of FAI was only weakly explained by the ENSO indices (linear regression for SOI, 101 degrees of freedom,β = -1, p <0.01, R-squared=0.077; linear regression for SST, 101 degrees of freedom, $\beta = 0.6$, p >0.1, R-squared=0.022). The results are in agreement with previous findings by Wich and Schaik (2000b), who found that the ENSO can induce higher frequencies of fruiting events although the effect was found to be weaker on Sumatra than on Borneo.

The mean FAI for all months was 9.7, with a minimum of 3.4 and a maximum of 18.27. No month was significantly different from the general mean (Kruskal-Wallis, df = 11, $\tilde{\chi}^2 = 10.66$, p = 0.47) (Figure A.8). A quick LMM with a Gaussian family distribution with multiple weather variables (night rain, day rain, cumulative rain last 4 days, average maximum temperature last 4 days, maximum temperature, minimum temperature, average temperature) explaining fruit availability was not better than a null model with only the random effects month and year. Due to collinearity between weather variables, the number of weather variables was reduced. But none of the tested LMMs was found to be better than the null model. However, a difference between years for FAI was visually observed, in that the year 2011 showed lower fruit availability values (Figure 2.6b).

Rain and temperature as weather phenomena are expected to influence movement on different spatio-temporal levels (Figure 1.1b). First, on Levels 1 to 2 on a weekly to even monthly scale by changing the fruit or food availability briefly. It should be differentiated from climatic differences such as different precipitation rates in the rainy season or influences of climatic oscillations over multiple yeas. However, both seasons and an influence of the ENSO was not observable in this data set. Although no seasons were observed, there was a surprisingly distinct period of higher amount of precipitation, resulting in lower temperatures (see above). The influence of the ENSO was previously described to be very weak for Suaq (Wich and Schaik, 2000a). Second, on Level 2 to 3 on an hourly or daily basis by influencing the movement of orangutans due to e.g. thermoregulatory reasons as well as by changing the movement e.g. due to a wet canopy (Parsons, 1999; Van Noordwijk et al., 2009). Heavy and prolonged rainfall was also described to temporarily inhibit the movement of individuals (Parsons, 1999).



(a) Precipitation and temperature



(b) Temperature and fruit availability

Figure 2.6 – **(a)** Mean precipitation [mm] and temperature [°C] over ten years for every month at the research station of Suaq. The derived mean maximum (evening and morning) (red dashed) and mean minimum temperature (evening and morning) (blue dashed) as well as the total average temperature (black dashed) is added as a secondary variable. Differences in total rainfall from the mean: linear regression with square root transformed total rainfall, 90 degrees of freedom, *** = p <0.0001, * = p <0.1, adj. $R^2 = 0.1047$. Differences in the monthly average temperature from the total mean: linear regression, 97 degrees of freedom, ** = p <0.01 , adj. $R^2 = 0.3245$. **(b)** Fruit availability and monthly mean temperature measurements [°C]. Categories for ENSO: neutral (-0.5 to 0.5), weak (with a ±0.5 to ±0.9 SST anomaly), moderate (±1.0 to ±1.4), strong (±1.5 to ±2) and very strong (>±2.0) either positive for El Niño- or negative for la Niña-events.

Chapter 3

Analysis I: Daily movement

(Level 2)

3.1 Methodology

3.1.1 Movement parameters

Day journey length

Many indicators can be derived from animal movement data sets. Many of them are used to analyse e.g. energetic costs, demographic patterns, distribution patterns, navigational skills, foraging behaviou,r and so on. An excellent overview for many of such metrics is given in Seidel et al. (2018)'s review. Similarly, the authors have grouped the parameters in path and space use metrics (Section 1.5). For path or movement metrics there are various parameters for an animal's moving trace. Mainly, they can be categorised into instantaneous indicators such as speed, turning angle and acceleration measured at the highest possible temporal scale (GPS steps) and relative indicators, computed over a whole day (GPS trajectory) such as mean speed, tortuosity and relating to orangutan studies e.g. DJL (Laube, 2014). The distance travelled by animals is one of the main metrics derived from GPS data and is often used to gain important ecological information (Rowcliffe et al., 2012). In orangutans, different day journey lengths are often considered as a sign of changing foraging strategies (Section 1.6) (Campbell-Smith et al., 2011; Wich et al., 2009). In general, the total travelled distance is a well established proxy for energy expenditure in orangutans (Knott et al., 2009).

Furthermore, it is used to distinguish different behavioural strategies relating to social factors such as mating strategies of males or philopatric range establishment of females Ashbury (2020); Atmoko et al. (2009). This total travelled distance is normally derived from each step between GPS positions. The step-length between consecutive spatial fixes is derived by the Euclidean distance. Subsequently, the sum of all these step-lengths is calculated for a defined period, in our case for the total follow length, which is a NN follow. The term DJL proved itself as very useful due to the ecological definition of the diurnal behaviour of a day journey between a morning nest and a night nest. Other names for the same concept are the total daily travel distance, travel length, distance moved per day. Alternatively, the term 'total daily travel distance' often used in other primatology studies can be used. It is important to mention that the actual distance traveled is mostly unknown and can only be approximated by summing the step-lengths of GPS fixes (Figure 2.2, first part of "in field"). Therefore, there is a discrepancy between the approximated DJL and the actual movement travelled by the animal (also to be seen in Figure B.2 in the Appendix). Hence, the effects of the mean sampling interval and the individual on DJL were analysed in an LMM and also by a separate analysis (Section 3.1.3).

Total displacement and tortuosity of movement

The diurnal behaviour of orangutans allows us to measure the distance between morning and night nests. This distance is measured as the Euclidean distance between these two GPS fixes (see also Figure B.2). The total displacement, sometimes also referred as nest distance, describes the functional movement of the full daily movement. In other ecological studies the concept is often used to distinguish migratory and territorial behaviour, where mostly the total displacement between each GPS fix and the starting point was used, the so-called 'net squared displacement', to categorise different migration phases (Bunnefeld et al., 2011; Calenge et al., 2009; Seidel et al., 2018). The displacement distance between nests of orangutans was already used as a proxy for total movement activity during different sexual phases of females in Tuanan. But compared to the total DJL, the TDD was not explaining differing movement patterns during different reproductive phases reliably (Ashbury, 2013). In this study, the TDD is of secondary importance but is used for measuring tortuosity. Tortuosity is a concept in movement ecology describing the number of turns and directional changes taken by an animal. It is a key parameter, which is used to measure searching behaviours and efficiency of movement e.g. between resources (Benhamou, 2004). In orangutan studies it was already used as a concept for differences in movement between age classes, where younger individuals were expected to move more inefficiently than adults (Schuppli et al., 2016). Nonetheless this study could not confirm this prediction. There are various methods of measuring tortuosity, where the effectiveness of many such measures is debated and they are not all of the same type. Examples include the intensity of habitat use, calculated by comparing the path length to the area underlying this path; the Straightness Index, calculated by the total displacement between start and end of follow divided by the actual measured distance travelled between the start and end (0 = highly tortuous, 1 = straight) (Equation 3.1); the sinuosity index which measures sinuosity, a concept which includes turning angles as well as step-lengths and compares it to a random search model for the evaluation of tortuosity (0 = straight, 1 = highly tortuous) (Equation 3.2); and the maximum expected displacement, which is similar to the sinuosity index and denotes a maximum expected displacement of a random search and relates it to the number of steps measured between the GPS fixes (0 = highly tortuous, 1 = straight) (Batschelet, 1981; Benhamou, 2004; Cheung et al., 2007; McLean and Skowron Volponi, 2018).

Tortuosity and sinuosity are often used interchangeably, but as we have seen there is a difference in the underlying concepts. Tortuosity is an umbrella term for sinuosity and straightness, where high sinuosity values denote heavily curved trajectories, while high straightness values indicate almost straight trajectories. Overall, measuring one aspect of tortuosity, for instance, the change in orientation does not have to correlate with, for instance, the straightness of a route; so, not all tortuosity measurements are measuring the same aspect. Any type of tortuosity parameter comes with its own limitations (Almeida et al., 2010; Benhamou, 2004; Cheung et al., 2007). The measure of sinuosity, for example, includes a scale dependency; therefore, the sinuosity index has, in contrast to the SI, a dimension. This means that e.g. the same movement trajectory pattern at different scales does not result in the same sinuosity index value. The length and size of a movement therefore influences the sinuosity index (Figure 3.3). This can be a welcome additional information but it can also be undesired when comparing different movements (Almeida et al., 2010). In our case we assume that the implicit normalisation of using standardised daily NN follows leads to meaningful and comparable values for the sinuosity of movement. To analyse eventual effects in the LMM, DJL was also tested as a fixed effect in the models.

$$Straightness = \frac{TDD}{DJL} \tag{3.1}$$

Simple Straightness Index (SI), developed by Batschelet (1981). Already used in orangutan studies, where it was referred to as 'ramble ratio'.

$$Sinuosity = 2\left[p(\tfrac{1-c^2-s^2}{(1-c)^2+s^2}+b^2)\right]^{-0.5} \tag{3.2}$$

Sinuosity Index (Benhamou, 2004), with p = average step-length, c = mean cosine of turning angles, s = mean sine of turning angles, b = coeff. of variation of step-length.

For this thesis the initial plan was to limit our analysis by focusing only on the Straightness Index (SI) calculated from the Total Displacement Distance (TDD) and the Day-journey-length or daily total-traveled-distance (DJL) (Equation 3.1). However, owing to the criticisms of Benhamou (2004) regarding the usage of the SI to capture goal-oriented searching paths of an animal, other tortuosity indices implemented in the trajr package in R were tested as well and compared to the SI. The sinuosity index, which is widely in use in many disciplines and is expected to give robust measures of tortuosity, was then further used for the analysis because I expected it to give better insights than the more simplistic SI. Factors influencing the tortuosity parameter performance such as positional errors or sampling frequency were assumed similar across all data points. For analysing effects of external and internal predictors a LMM was fitted (Section 2.1.4) and analysed. As response variables the movement parameters were used, namely our primary movement parameters, the DJL and SI. The explanatory variables were derived from the main data set and the additional data sets (Figure 2.2). They can be divided into external and internal factors. The weather variables, including total rainfall, temperature (average, minimum morning, minimum evening, maximum morning, maximum evening), the water level as a proxy for rainfall over a longer time period; the fruit availability; and the number of fruit trees visited are external factors. Internal factors analysed were age (derived from the approximation of birth date), class of the focal (adult female, infant, flanged male, unflanged male), and the age of the currently youngest offspring. The variables were all included in a full LMM and compared to a null model with only random effects (Section 2.1.4).

3.1.2 Workflow

The full data set was filtered to retain only found/lost-points, nests, ranging points and trees (Section 2.3), which gave us a total of 1314 follows and 27058 GPS fixes. For the analysis of feeding trees and the comparison to tortuosity the full workflow was also checked when dropping the tree GPS points. The results did not deviate if only 30 min ranging points were taken, therefore I kept them in the final analysis. Just the mean time lag was slightly influenced when using some intermediate tree GPS points. But the following general results did not change. Previously defined outliers, long calls, experiments and other points were excluded. As a normalisation step, only NN follows were considered which reduced the amount of data by nearly half (640 follows, 17961 GPS fixes). For the resulting data set, for every GPS point the distance to its next (same follow number, temporally closest) GPS fix was calculated. The DJL was calculated using the sf-package in R. Additionally, the step-wise time lag, speed, and turning angle for every point was calculated. This resulted in a data set of 640 follows for all tracked focals in Suaq Balimbing. Moreover, the TDD was calculated. Calculating the ratio of the DJL and the TDD produced the SI for each follow. Then the sinuosity index was calculated for each follow with the trajr (1.4.0) package (McLean, 2020). The predictor variables (Random: date, individual; External: temperature, precipitation, water level, FAI; Internal: Age-sex class, age, dominance category, age of current offspring) were added. The dominance category is derived from contest interactions between females for example when feeding in a large productive fig tree (Knott et al., 2008) (1 equals to highest dominance and 4 to lowest). Dominance correlated highly with the age of the individuals. Therefore it was used interchangeably. Last but not least the number of fruit trees visited for every follow was calculated and added as a variable. All the movement parameters were then analysed with LMMs and model fits were visually inspected.

3.1.3 Uncertainties of travel distance and straightness

There is a discrepancy between the measured movement and the real movement of an animal (2.2). Rowcliffe et al. (2012) rightly criticised the often overlooked underestimation of daily travel distances due to too low sampling rates, which leads to misleading results. Few studies attribute the uncertainty of measured travel distances. Rowcliffe et al. (2012) analysed the movement of 10 Panamanian forest mammal species and tried to approximate the underestimation of daily travelled distances. They found an underestimation of 63 to 93% compared to the approximate real high frequent measured travel route. Other authors found less deviation of the true daily traveled distance (Dewhirst et al., 2016; Musiani et al., 1998). Sennhenn-Reulen et al. (2017) looked at terrestrial baboons and found that the DJL were on average 7-35% shorter than the true movement for sampling rates of below 120 min. Furthermore they found that sampling rates over 120 min had a less pronounced effect on the underestimation of daily travelled distances which is in agreement of the findings of Rowcliffe et al. (2012). Rowcliffe et al. (2012) notes that the daily travel distances can only be estimated exactly with several GPS fixes per minute. This is an impossible value for conducting foacal animal follows. However, he also notes that the distortion is generally less for larger species, as in our case (Rowcliffe et al., 2012). The derived SI used in this thesis is calculated from the DJL and is therefore affected similarly as the travel distance itself. Movement tortuosity can be positively affected when the sampling rate is very short because of the possible accuracy of GPS measurements. On the other hand, tortuosity is negatively affected by longer sampling regimes (which means higher straightness, lower sinuosity) when we are not able to catch local tortuous movement anymore. In our case this is more likely the case.

There is certainly an inherent systematic underestimation of travel distances based on the sampling rate in our study. The sampling rate of 30 min is relatively high compared to other animal movement studies (Sennhenn-Reulen et al., 2017; Zehnder et al., 2018). To analyse the effect of such an error there was an opportunity to look at few follows (n = 18) from December 2010 until May 2011 where the sampling rate was 5 min instead of 30 min. To know how much the movement parameter SI and DJL are affected, a sub sampling of the follows was executed. Because the data set is not harmonised and the sampling rate is mostly 30 min (Figure 3.2.2) but not always the resulting relationship was analysed by a visual assessment. Furthermore the mean time lag of a follow was used as an explanatory variable for the LMM's trying to explain the values of the movement parameters. If we find a strong influence of the mean sampling interval time this would result in incomparable day journeys. But we expect that the standardised and well applied sampling regime lead to comparable day journeys with little variation in time lags and therefore follow specific variation for this sampling error.

3.1.4 Movement between feeding trees and movement patterns during the day (Level 3)

To further analyse how the movement behaviour of orangutans is influenced by external or internal factors we dive into Level 3 of analysis, which has so far never really been done in any movement ecology study about orangutans. To get insights on the movement patterns related to fruit availability, the same overall analysis was carried out by just selecting the nest points and tree points and deriving the number of feeding trees, the SI and the DJL per follow. The idea was especially that potential changes of external or internal factors may change the straightness and distance of movement between feeding trees. Feeding trees therefore were hypothesised to be main factors of influencing movement patterns, which was previously used as an explanation of bigger ranging patterns in Suaq (Singleton et al., 2009). But a preliminary assessment of the methodology of analysing the day journey by only considering feeding trees was found to be not so meaningful. By only looking at such tree-to-tree trajectories over a full day at least an observable change in the tree-to-tree length, for example due to change in FAI, could be observed. That could, for example, mean that an orangutan planned to visit feeding trees which are nearer to each other when fruit is more abundant. But calculating the straightness index for a full follow of only connecting feeding trees is arguably less meaningful when the goal is to measure the efficiency of movement between feeding sources. For being able to still analyse potential changes in movement between feeding trees when internal or external factors change it was hypothesised that there is a potential difference in movement between feeding trees and other movements not directly linked to feeding. Although orangutans spend about 50 % of their time feeding it could be argued that other factors than feeding might play a role when they are travelling from place to place (Morrogh-Bernard et al., 2009). Orangutans' daily movement path can potentially be seen as a random or planned search pattern where feeding trees are checked off.

Therefore, the first hypothesis was that the straightness between two feeding trees must be higher compared to any random selection of movement on Level 3 (Point A to Point B). All feeding-tree-A to feeding-tree-B movements were retrieved and their TDD, their SI, the time that passed for relocating, and the number of GPS fixes taken between relocations was calculated. The number of GPS fixes (= window size, GPS fixes between tree A to tree B) was included because we need to correct for the number of steps when comparing the directness and distance between points. Additionally, a random subsample with the same window size was taken from the full data set to compare the found travel distances, SI, and travel times to a random selection during follows. The random selection was repeated and changes in results were checked.

The second hypothesis was that the movement between feeding trees may be influenced by internal and external factors, for instance, that higher values of the FAI lead to higher tortuosity and therefore less movement efficiency between feeding trees. The two samples were therefore not only statistically compared with each other, but the influence of explanatory variables on SI was analysed similarly as for the main analysis of full follows, whereas here the window size was additionally included as a random effect.

The movement patterns by time of day were analysed by calculating the mean distance moved for a specific time window. The follows had to be harmonised and only distances were considered when the full time window was available. For example, a follow might have a morning nest point at 7:23, a range point at 7:30, 7:59, and 8:30. For a time window of 15 minutes, this follow would have been subsampled, where the first point would be placed at 7:30. The second point would then be linearly interpolated from the trajectory at 7:45, the third point likewise at 8:00, and so on. The first 7 minutes of the follow would not be considered because only movement for a full time window was included to be able to compare temporally standardised movements and not having short time snippets with short distances. An alternative would be to always start with the first point of a follow and then compare the follows independently of time of day to find any daily routines. The time window was either chosen to be 30 minutes or 15 minutes, depending on how much the data was smoothed for visual assessment. For this analysis all follows rather than only NN follows were included.

3.2 Results

An overview of all scatterplots and Pearson's correlation coefficients of the dependant movement parameter indicators and the used independent explanatory variables can be found in the Appendix (Figure B.4).

3.2.1 Results of subsampling densely sampled follows

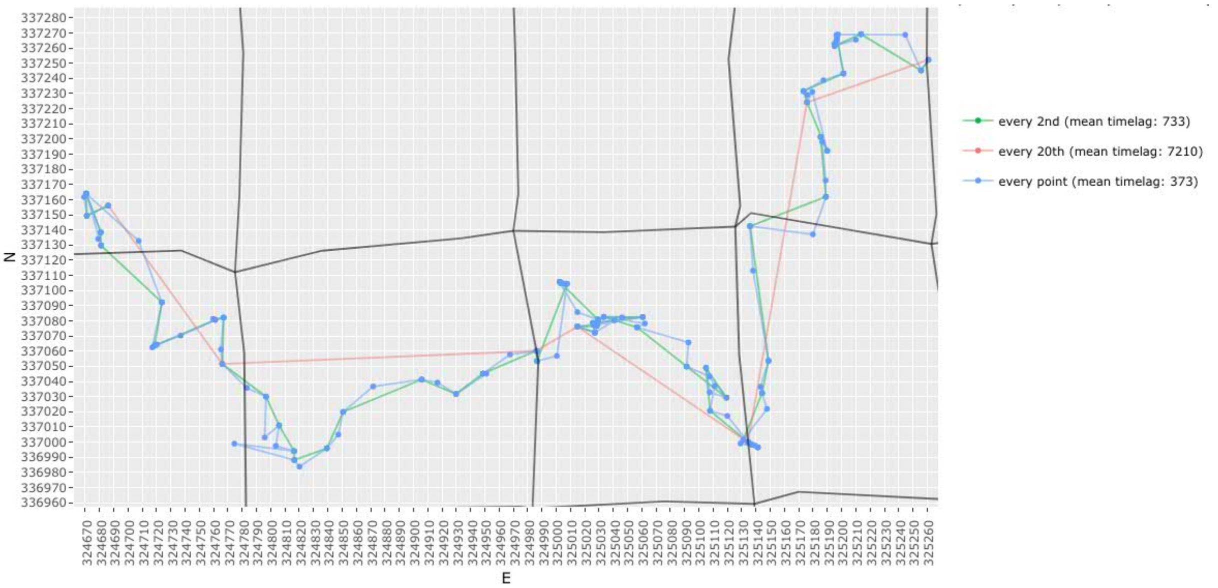
As expected the subsampling of follows that were initially sampled at a 5-minute interval showed that DJL and the SI is heavily affected by the sampling regime. Average decrease when every second point was skipped was -20 % (± 5 %), which equals to a doubling of the sampling interval from 10 to 20 minutes. Average decrease when again every second point was taken, which equals to every fourth point, was an additional -15 % (± 3 %), which equals to again doubling the sampling interval from 20 to 40 minutes. Therefore, the DJL is decreasing strongly with coarser sampling intervals. Probably missing the underlying rambling behaviour with coarser sampling intervals is the reason for such a decrease. Such local rambling behaviour is expected to be real and not mainly an effect of GPS positional uncertainty or noise (Figure 3.1a). The bias was stronger in longer DJL follows and weaker in shorter follows. This was expected, because if rambling stays undetected with coarser sampling intervals the total distance of rambling is expected to increase exponentially for longer follows (due to movement being two-dimensional). In general fine-grained rambling behaviours are detected by a 5-minute sampling regime. General movement directions are well captured by the used 30-minute sampling interval. With sampling intervals above 45 minutes it appears that fundamental positional changes are lost. This can be seen in Figure 3.1b. Unstable decrease of DJL which is seen by volatile swings at around 45 minutes indicates that, for example, the subsample of every 8th point misses a movement, whereas an even coarser subsample, for instance the one with every 10th GPS fix luckily captures the same quick movement. But this shows that GPS points are lost on this coarsse sampling level, which has a bigger impact on the overall DJL.

For the SI we see similar results with increasing straightness until total straightness, which happens when the follow was so coarsely subsampled that only the start to end points remained. The strongly varying values above 45 minutes can be detected as well, which is no surprise as the straightness is derived from the travel distance. Overall, the follows did not change strongly when compared to each other when reaching the level of our usual sampling regime of 30 minutes. It was checked how much the DJL measured at a sampling rate corresponding to about 30 minutes (i.e., every 4^{th} point, practically it was 40 minutes) does explain the highest resolution of the real walk (i.e., every point). A linear regression model with the DJL of the densely sampled data set (median 5 minutes) as dependant and the DJL of the coarsely sampled data set (median 30 minutes) as predictor variable was fitted. All assumptions, such as a more or less linear relationship, homoscedasticity of errors, independence of observations, and normality of errors were met. The full model could explain 86% of variation and for every 1 metre measured with a longer sampling interval (30 min) the DJL of the higher temporal resolution corresponded to a change of 1.3 m (linear regression, 16 degrees of freedom, $p = 0.00001$, R-squared=0.8687). Similarly, a bootstrapping analysis for the overlap of the original trajectories and the subsampled trajectories showed a decrease of 25±3 % when the mean sampling interval was around 30 minutes. The subsampling of movement paths did not result in big changes of the representation of the follows (Figure 3.1a). While smaller rambling behaviours for this specific track are lost first during the subsampling process — see e.g. the south-western part of the follow — the overall movement remains visible. Even when taking a point only every hour, the movement pattern remains almost clear. After subsampling at an even coarser rate, more pronounced shortenings are happening.

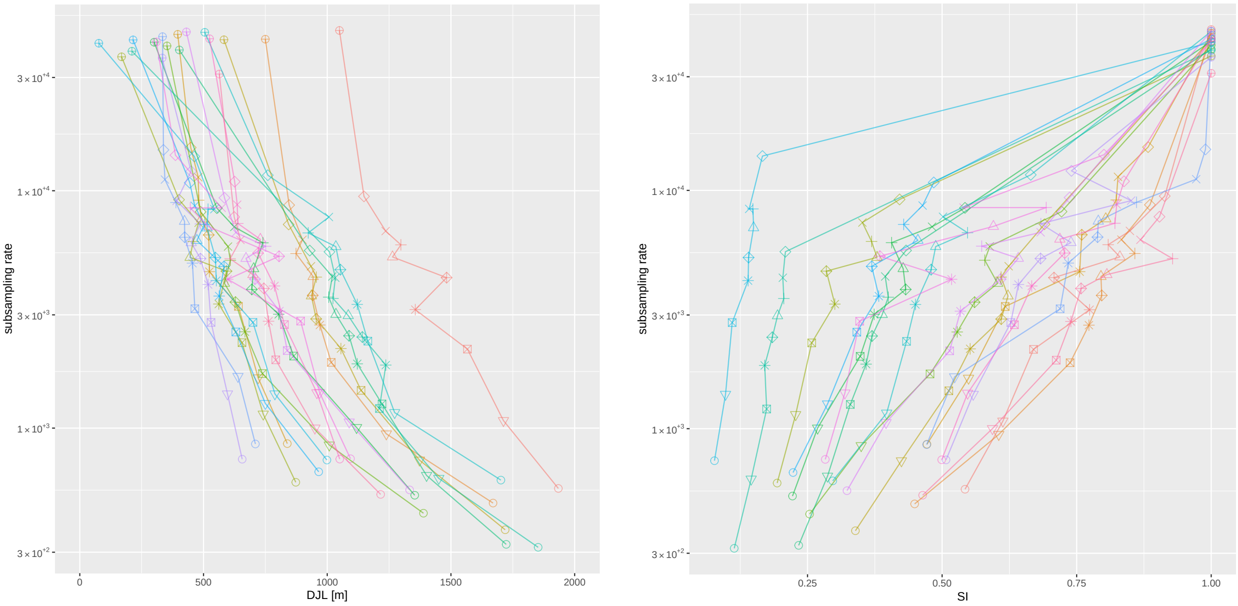
3.2.2 Daily travel distances

Overview and age-sex classes

A total of 640 NN follows were analysed. The total number of follows consisted of 407 follows of adult females, 17 follows of infants, 73 follows of independent immatures, 102 follows of flanged males, and 41 follows of unflanged males. An overview of the data per each age-sex class is given in Table 3.1. The full table and a visual overview for every individual is available in the Appendix (Table B.1). For adult females, the estimated age ranged from 16 to 77 years. The average age of their offspring was 3.3 years, which is approximately half of the weaning age threshold. For males, there were no approximations of the date of birth



(a) Subsampled follows (coordinate grid resolution = 10 m)



(b) DJL

(c) SI

Figure 3.1 – Overview of subsampling of 18 high frequency follows. The follows were subsampled by taking every 2nd, 4th, 6th, 8th, 10th, 12th, 14th,20th, and finally only start and end points. **(a)** Follow 687 of Friska, a mother. In blue we see the original movement path with an approximated average sampling rate of 10 min (median and intended sampling rate is 5 minutes), in green we see the same follow after selecting only every fourth point, which should reflect a sampling rate of around 40 minutes (although all sampling rates are generally higher). **(b)** We can see that there is a short levelling at about 50 minutes, where the DJL rapidly decreases and stronger variations due to subsampling occur. Probably by reducing the sampling interval, first the rambling behaviour is smoothed and the decrease in distance is not as strong and more or less constant. Then after about 15 minutes we see a strong drop in DJL. This indicates that then the movement trajectories are getting smoothed not only locally but more than locally. **(c)** The same is seen for the SI of the orangutan follows: a constant increase in linearity where at about 50 minutes most disturbances occur due to subsampling.

available and independent immatures were at the expected average age at the start of sexual activeness. Interestingly, the estimated age of the infant class was very high. This probably reflects some misclassification of follows. It is often the case that accidentally the mother and infants are confused in the data. Therefore, any results for infants have to be evaluated carefully.

The average time lag between fixes was slightly under 30 minutes, with a mean step-length of 34.7 m. In less than 2.5 % of follows the step-length was over 130 m. Shorter step-lengths occurred more often than longer ones (Figure B.7). It was tested if there is a difference between age-sex classes for the mean time lag between fixes, which could originate from different factors while sampling when following an individual (losing and refinding a focal, spurious deviations from the regular sampling interval for a follow, etc.). It was expected that there should not be any difference because there was no such feedback from the field, which was confirmed (Kruskal-Wallis, df = 4, $\tilde{\chi}^2 = 4.5$, p = 0.33). On average the follows consisted of 28 GPS fixes. This average is higher than expected because few follows had a very high sampling rate. The derived movement parameter were all tested if they differed between age-sex classes. The total sum of turning angles, which is another very simple tortuosity index, showed no difference between age-sex classes (Kruskal-Wallis, df = 4, $\tilde{\chi}^2 = 1.16$, p = 0.883). The TDDs from morning nests to night nests were not statistically significant different (Kruskal-Wallis, df = 4, $\tilde{\chi}^2 = 7.14$, p = 0.13), but males had slightly longer TDDs on average, with unflanged males showing the biggest locational change. Interestingly, infants staying with their mother showed similarly high values as well, but sample size is weak for infants (n-follows=17).

The DJL, our main movement parameter, was on average 884.12 ±338 m. It was clearly different between age-sex classes (Kruskal-Wallis, df = 4, $\tilde{\chi}^2 = 13.523$, p = 0.009). Independent immatures and unflanged males had also high variations of DJL, with especially more frequent longer follows. We have to consider that these data are unbalanced but still substantial compared to earlier orangutan studies about travel distances (Digiorgio and Knott, 2012; Vogel et al., 2017; Wartmann, 2008). Nonetheless, on average DJL of unflanged males was found to be around 150 m longer than for adult females.

The SI, derived from the TDD and DJL, was also different between age-sex classes (Kruskal-Wallis, df = 4, $\tilde{\chi}^2 = 11.19$, p = 0.025), and likewise was average speed (Kruskal-

Wallis, df = 4, $\tilde{\chi}^2 = 15.72$, p = 0.0034). Comparing the values of the SI across age-sex classes, infants had the highest values, whereas all other classes tended to be similar and independent immatures had the lowest values for straightness.

The average speed values again followed the differences in DJL. The highest value was reached by the unflanged males and independent immatures becoming.

The sinuosity index as an alternative to the SI showed to be different for the different age-sex classes (Kruskal-Wallis, df = 4, $\tilde{\chi}^2 = 10.67$, p = 0.03). A pairwise t-test and visual inspection showed that sinuosity was highest for infants and similar for adult females and flanged males. The lowest values were found for independent immatures and unflanged males. Further details are presented in the following sections.

Table 3.1 – Overview of day journey length.

class	n^1	age	age off.	* DJL [m]	TDD [m]	* SI	* sinuosity	* $speed^2$	length	$^{\circ 3}$	trees	points	sampl.rate
unflanged male	41			1002±397	465±265	0.46±0.19	0.22±0.06	0.09±0.19	11:05:10	4465	2	27.1	00:25:52
independent immatures	73	10.6		980±336	398±195	0.42±0.17	0.23±0.06	0.088±0.17	11:07:54	4631	4	28.4	00:25:40
infant	17	8.1		829±175	465±160	0.56±0.16	0.25±0.05	0.076±0.16	10:56:00	4489	4	28.1	00:24:47
flanged male	102			880±371	439±288	0.48±0.19	0.24±0.06	0.08±0.19	10:59:51	4459	3	26.7	00:26:06
adult female	407	41.1	3.5	858±323	394±213	0.46±0.18	0.25±0.06	0.078±0.18	11:03:55	4695	3	28.4	00:26:05

^{1}: number of follows, ^{2}: [km/h], ^{3}: sum of turning angles [°], *: difference between age-sex classes are on significance level

Mixed linear model explaining DJL

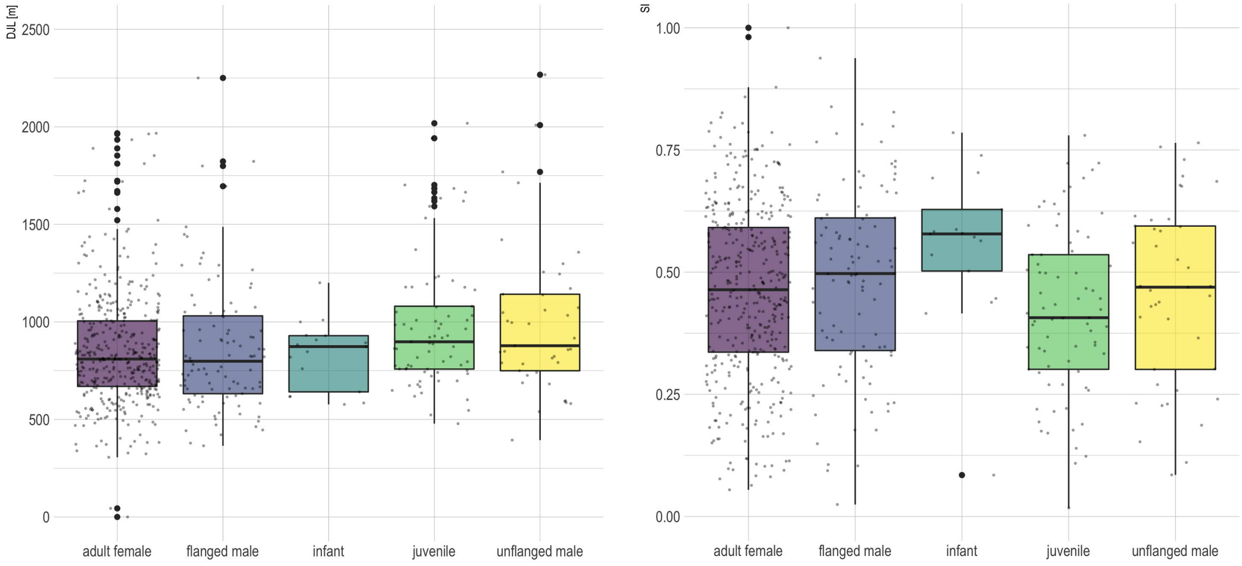
First, the DJL was not found to be influenced by the mean sampling rate of each follow (Spearman's rho, r_s = -0.051, p = 0.2). Nonetheless, the sampling rate was included as an explanatory variable in the linear mixed effect model (See model Table 3.2). Where it confirmed our initial analysis and DJL was mostly negatively impacted by larger mean time lags, but the variable still was not a statistically significant explanatory variable for DJL (p Value over 0.1). All predictors and random effects were chosen a priori. Random effects were included for controlling for pseudo replication. The DJL showed some variation through the year. An LMM where month was used as a explanatory variable and year as a random effect showed that the months May, June and August yielded more negative values than expected (May -107 m, p = 0.09; June -133 m, p = 0.049; August -232 m, p = 0.025) and in December DJL was longer than expected (December +179 m, p = 0.025, marginal r^2 = 0.09) (Figure B.11). Differences between years, on the other hand, were smaller and explained less of the variation.

Age and dominance was excluded in the selected model and the full model because there were many missing values and the sample size would have been much smaller for the selected model if age or dominance was included (If included they both showed a not significant negative effect on DJL e.g. -26 m per dominance class). The full model was fitted and collinearity among the variables (VIF) was not a problem (Table 3.2 a)).

Due to high colinearity among most weather variables (Figure B.10) several of the weather variables were deselected. The temperature variables correlated highly and the average total temperature explained most of the other temperature variables well (max. morning, max. evening, avg. max, avg. minimum). Only the minimum temperature in the morning and evening was not strongly correlated with the average temperature. To reduce the number of variables, all except the average temperature were excluded from the analysis. The resulting variance of inflation factor for all explanatory variables ranged between 1 and 1.2, which is acceptable. The selected model showed only a trend for age-sex classes, as already described before. Where unflanged males were predicted to travel 182 m more and independent immatures were predicted to travel 131 m further than adult females. Rain during the day had a positive effect on DJL, whereas rain at night had a negative effect but both were statistically not significant (p >0.1). Temperature had a positive effect on DJL but was also not statistically significant. All weather variables were not statistically significant. When including two variables considering the current weather of the last four days, total precipitation (last four days) and mean maximum temperature (last four days), still no statistical relation to DJL could be found.

Fruit availability had a slight negative effect on DJL but did also not improve the model (Table 3.2 a)). Of the tested explanatory variables only the age class remained a clear explanatory variable, nonetheless the model was not significantly better than the null model (p = 0.11) when correcting for month-year and individual differences. Overall, no effect of fruit availability and weather variables on DJL were detected. A random effect ANOVA, which deletes random effects and compares the models, showed that the month-year was a strong random effect, whereas the focal had little explanatory power in the selected model (ranova from the lmerTest package; Δ $\text{AIC}_{\text{focal dropped}} = 8707.47$, p = 0.22; Δ $\text{AIC}_{\text{month-year dropped}} = 8740.04$, p <0.001) (Figure B.13). Intraclass Correlation (ICC), which is the expected correlation of two follows within the groups of our random effects, was 9 % for focals and 11 % for month-year groups (Lüdecke, 2021). Therefore, differences between individuals did not explain much more of DJL when having the age-sex class of the individuals in the model. Overall the selected model only explained around 20 % of variation in DJL (conditional $R^2 = 0.198$), where the fixed effects only explained around 3 % of variation (marginal $R^2 = 0.034$). The random effects, namely individual differences and monthly variation, explained the most (see ICC above).

When focusing on females only the inclusion of the age of the offspring as an explanatory variable clearly improved the model (Table 3.2 b)). The age of the offspring correlated positively with DJL and an increase of the offspring age by a year explained an increase of around 34 m in DJL (Figure 3.3d). The selected model for only the data set of females explained around 16 % of variation (conditional $R^2 = 0.157$), whereby the fixed effects and mainly the age of the current offspring explained around 8 % of this variation (marginal $R^2 = 0.086$). The selected model was better than the null model with only random effects.



(a) **(b)**

Figure 3.2 – (**a**) DJL of age-sex classes. (**b**) SI of age-sex classes.

Table 3.2 – Regression models trying to explain travel distances per day for all age-sex classes and for females with offspring only, respectively. The marginal R^2 (M-R^2) equals to the marginal coefficient of determination which represents the variance explained by the fixed effects whereas the conditional R^2 (C-R^2) represents the variance explained by the full model. The p-values for random effects equals to a likelihood ratio test of random effect deletion.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	DJL of all age-sex classes	Intercept	intercept	645.54	-231.86 – 1522.94	0.149	-
	n = 610	Day rain	Predictor	0.12	-1.87 – 2.10	0.909	1.0
	P = 0.10998	Night rain	Predictor	-0.67	-1.56 – 0.22	0.14	1.0
	M-R^2 = 0.034	Average day temp.	Predictor	11.17	-21.65 – 43.99	0.505	1.0
	C-R^2 = 0.199	FAI	Predictor	-1.26	-17.56 – 15.04	0.88	1.0
	Family = Gaussian	ASC: Flanged male	Predictor	37.45	-63.91 – 138.80	0.469	1.2
		ASC: Infant	Predictor	32.84	-154.85 – 220.54	0.732	1.1
		ASC: Independant immature	Predictor	130.42	24.45 – 236.39	**0.016**	1.2
		ASC: Unflanged male	Predictor	182.27	57.09 – 307.45	**0.004**	1.2
		Mean time lag	Predictor	-0.06	-0.21 – 0.09	0.439	1.0
		Focal	Random	-	-	0.22445	-
		Month Year	Random	-	-	**<0.001**	-
b)	DJL of only females	Intercept	intercept	476.68	-657.38 – 1610.74	0.41	-
	n = 340	Day rain	Predictor	-0.24	-2.46 – 1.98	0.831	1.0
	P = 0.004658 **	Night rain	Predictor	-0.66	-1.99 – 0.67	0.33	1.0
	M-R2 = 0.07	Average day temp.	Predictor	10.76	-31.51 – 53.03	0.618	1.0
	C-R2 = 0.14	FAI	Predictor	-10.88	-27.73 – 5.97	0.206	1.0
	Family = Gaussian	Age of current offspring	Predictor	33.52	17.07 – 49.97	**<0.001**	1.0
		Dominance category	Predictor	26.17	-10.96 – 63.29	0.167	1.0
		Focal	Random	-	-	1	-
		Month Year	Random	-	-	**0.00052**	-

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; bold = significance level reached

3.2.3 Tortuosity

Straightness index

The same independent predictors were used for this model as for the DJL model, trying to explain the straightness of movement (Table 3.3 a)). The straightness index was not heavily influenced by the sampling interval (Spearman's rho, $r_s = 0.053$, p = 0.18). Therefore I did not include it in the model this time. The combination of month-year and focals was also used as random effects. Variation between months was small only in April the SI was a bit higher and statistically different from the other months (LMM with year as random effect, April +0.08, p = 0.04) and years did not differ and explain SI at all. In contrast to the selected model for DJL the focal had a stronger effect explaining SI (ranova; Δ $\mathrm{AIC}_{\text{month-year dropped}}$ = -261.9, p = 0.5; Δ $\mathrm{AIC}_{\text{focal dropped}}$ = -249.5, p <0.001) (Figure B.13). The ICC for the random effect of focals was again around 9 %, whereas for month-year combinations it was only 2 %. Therefore, only the focal had an effect on the SI.

The fitted model with all explanatory variables was not better than the null model with only random effects. Again, only dominance was used because dominance categories and age are highly colinear. A slight positive effect of age and lower dominance on the SI was found (Table 3.3). The selected model showed a subtle but not significant positive effect of

Table 3.3 – Statistical models trying to explain straightness of movement per day for all age-sex classes and for females with offspring only, respectively.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	Straightness Index of all age-sex classes	Intercept	intercept	0.2507	-0.22 – 0.72	0.300	-
	n = 610	Day rain	Predictor	-0.0003	-0.00 – 0.00	0.652	1.0
	P = 0.75	Night rain	Predictor	0.0003	-0.00 – 0.00	0.187	1.0
	M-R^2 = 0.009	Average day temp.	Predictor	0.0070	-0.01 – 0.02	0.443	1.0
	C-R^2 = 0.12	FAI	Predictor	0.0021	-0.00 – 0.01	0.507	1.0
	Family = Gaussian	ASC: Flanged male	Predictor	0.0151	-0.05 – 0.08	0.654	1.3
		ASC: Infant	Predictor	0.0645	-0.05 – 0.18	0.254	1.2
		ASC: Independant immature	Predictor	-0.0142	-0.08 – 0.05	0.678	1.3
		ASC: Unflanged male	Predictor	-0.0007	-0.08 – 0.08	0.985	1.2
		Focal	Random	-	-	0.002	-
		Month Year	Random	-	-	0.370	-
b)	Straightness Index of only females	Intercept	intercept	**0.4491**	-0.26 – 1.15	0.211	-
	n = 340	Day rain	Predictor	**-0.0007**	-0.00 – 0.00	0.291	1.0
	P = 0.83	Night rain	Predictor	-0.0001	-0.00 – 0.00	0.869	1.0
	M-R2 = 0.008	Average day temp.	Predictor	0.0008	-0.03 – 0.03	0.952	1.0
	C-R2 = 0.087	FAI	Predictor	0.0023	-0.01 – 0.01	0.636	1.0
	Family = Gaussian	Age of current offspring	Predictor	-0.0006	-0.01 – 0.01	0.914	1.0
		Dominance category	Predictor	-0.0120	-0.05 – 0.03	0.533	1.0
		Focal	Random	-	-	0.210	-
		Month Year	Random	-	-	0.050	-

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; bold = significance level reached

night rain, higher temperatures and FAI, and a negative effect of day rain on the SI. Age, when not omitted, did also show a positive slope. The age-sex class of infants showed higher straightness, although the sample size was small and differences were too small to show a clear trend. Independent immatures, on the other hand, for whom the sample size was a bit larger, showed slightly lower straightness.

For the model where only females were considered the inclusion of age (negative slope) and age of offspring (positive slope) did not improve the model and the selected model was still not better than the null model (Table 3.3 b)). A step-wise backward selection of all possible explanatory variables did also show that none of the models was statistically better than the null model with only the random effects. A quick comparison with the TDD, which is one of the variables used to calculate the SI, shows that both parameters depict similar patterns. The fitted LMM showed that both were not well predicted by any of the predictors used. The only difference found was, that TDD was positively influenced by the age of the current offspring and an LMM with the age of the current offspring as the predictor was better than the null model.

Sinuosity index and comparison of movement parameters

To support the findings of the straightness index as the first descriptor of tortuosity, the sinuosity of movement was calculated as well (Equation 3.2). The values of sinuosity showed a negative correlation with the mean time lag (seconds) of the follows (Spearman's rho, $r_s = -0.24$, $p < 0.001$). This correlation is mainly influenced by much lower values and some high values of mean time lag. Nonetheless, this follows the logic of more tortuous movements with a denser sampling rate. Nevertheless, the mean sampling interval was as before excluded in the selected models because the number of feeding trees were colinear with the mean time lag. The reason for that is that the approach was to leave the feeding trees in the data set as additional waypoints, but as a result small fluctuations of the mean time lag were the result of this dependency on the number of feeding trees. Age and dominance did not improve the model and were excluded. If included, dominance and age showed higher values for more dominant and older females.

The selected model with the DJL was better than the null model with only random effects (Table 3.4 a)). The variance of inflation factor was checked to see if multicollinearity is a problem. The value varied around 1 which is good. We can see that the model is better than the null model and that the sinuosity of movement was bigger when more trees were visited during the day journey (Figure 3.3h). Comparing the number of fruit trees with the dimensionless SI a similar pattern was found, namely, that more fruit trees were visited when the movement was more tortuous (Figure 3.3g).

A model fitted using the selected explanatory variables showed that unflanged males probably move in a less tortuous fashion by a factor of 2 % ($p<0.05$) (Table 3.4 a)). Independent immatures similarly moved less tortuously ($p < 0.1$). However, when using the DJL for adjusting the scale dependency of the sinuosity index the differences between age-sex classes disappeared. Therefore, the difference in sinuosity between age-sex classes could probably be traced back to the differences in DJL between classes because the sinuosity index is scale dependent. Still if we consider that sinuosity partially also measures scale and distance travelled than unflanged males and independent immatures showed statistically significant difference. The ICC for the random effect of focals was around 4 %, whereas for month-year combinations it was only 10 %. Overall, the selected model explained around 53 % of the variation in sinuosity (conditional $R^2 = 0.567$) where the fixed effects explained most of it (marginal $R^2 = 0.561$).

When focusing on females only, the age of offspring did negatively impact (-0.7%) the sinuosity of movement (Figure 3.3e). The selected model for females better than the null

Table 3.4 – Statistical models trying to explain sinuosity of movement per day for all age-sex classes and for females with offspring only, respectively.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	Sinuosity of all age-sex classes	Intercept	intercept	0.38	0.2680 – 0.4920	**<0.001**	-
	n = 610	Day rain	Predictor	-0.0002	-0.0004 – 0.0001	0.229	1.008767
	p <0.0001	Night rain	Predictor	-0.0001	-0.0002 – 0.0001	0.3	1.021046
	M-R^2 = 0.527	Average day temp.	Predictor	-0.0016	-0.0058 – 0.0027	0.466	1.037807
	C-R^2 = 0.533	Number of fruit trees	Predictor	0.0053	0.0043 – 0.0063	**<0.001**	1.055333
	Family = Gaussian	FAI	Predictor	0.0005	-0.0010 – 0.0020	0.495	1.047529
		ASC: Flanged male	Predictor	0	-0.0099 – 0.0098	0.993	1.097366
		ASC: Infant	Predictor	-0.0056	-0.0275 – 0.0163	0.614	1.052394
		ASC: Independant immature	Predictor	-0.0015	-0.0129 – 0.0099	0.798	1.082264
		ASC: Unflanged male	Predictor	-0.0019	-0.0160 – 0.0122	0.79	1.069657
		DJL	Pr. correct scale. dep.	-0.0001	-0.0001 – -0.0001	**<0.001**	1.042747
		Focal	Random	-	-	0.77	-
		Month Year	Random	-	-	0.6	-
b)	Sinuosity of only females	(Intercept)	intercept	0.3734	0.2053 – 0.5415	**<0.001**	
	n = 340	Day rain	Predictor	0	-0.0003 – 0.0004	0.956	1.042266
	p <0.0001	Night rain	Predictor	-0.0001	-0.0003 – 0.0001	0.284	1.039526
	M-R2 = 0.469	Average day temp.	Predictor	-0.0006	-0.0069 – 0.0057	0.844	1.044287
	C-R2 = 0.472	FAI	Predictor	-0.0002	-0.0021 – 0.0018	0.869	1.039923
	Family = Gaussian	Age of current offspring	Predictor	-0.0027	-0.0052 – -0.0002	**0.034**	1.171131
		Dominance	Predictor	-0.0034	-0.0105 – 0.0038	0.356	1.029633
		Number of fruit trees	Predictor	0.0053	0.0038 – 0.0068	**<0.001**	1.098676
		DJL	Pr. correct scale. dep.	-0.0001	-0.0001 – -0.0001	**<0.001**	1.115295
		Focal	Random	-	-	0.48	-
		Month Year	Random	-	-	1	-

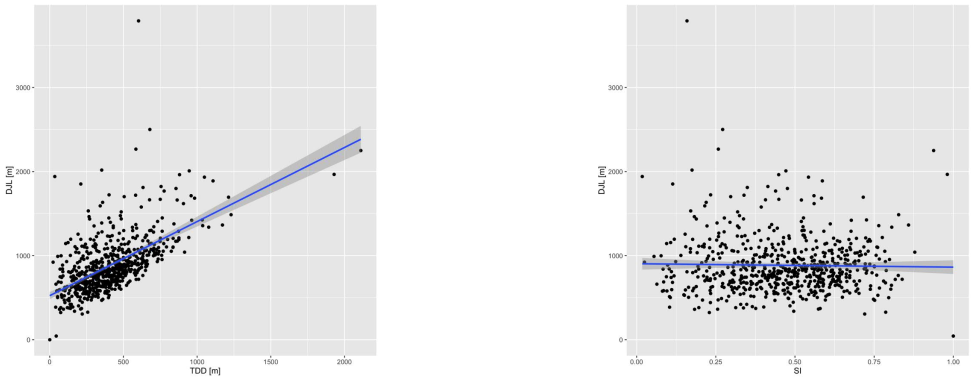
$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; bold = significance level reached; Statistical variables info's see first table

model when using the age of the current offspring as the only predictor (Table 3.4 b)). Number of fruit trees also positively affected sinuosity of movement. We have to consider that a high percentage of explanatory power of fixed effects stems from the higly significant DJL predictor. Both models without DJL as random effect were not significantly better than the null model but the trends were the same.

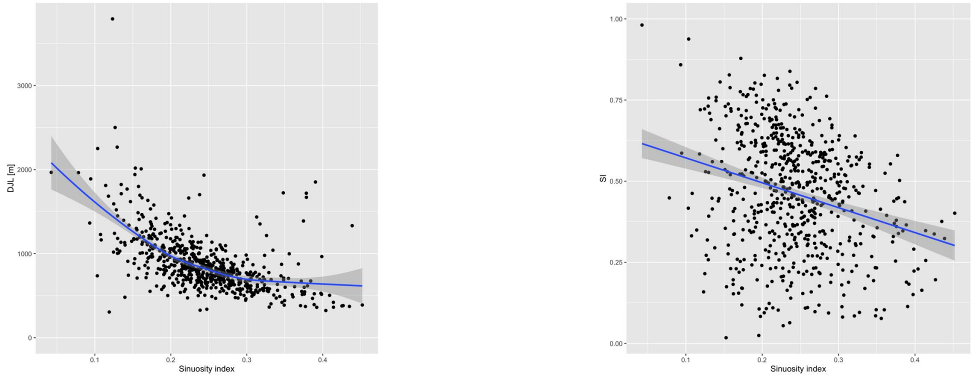
3.2.4 Fruit trees visited

The mean number of fruit trees visited per follow was 3.2 and the maximum was 66 (1$^{\text{st}}$ Qu: 0, 3$_{\text{rd}}$ Qu: 4.25). When neglecting the follows without any tree visited the mean was 7.8 trees (1$^{\text{st}}$ Qu: 3, 3$_{\text{rd}}$ Qu: 9). The number of fruit trees visited varied over months. Nearly all months were substantially different from each other considering the number of fruit trees (tested with LMM and t-tests using Satterthwaite's method; see also Figure B.18). There were also substantial differences between years. Comparing the null models with all combinations of focal, month and year showed that the year alone explains most of the variance.

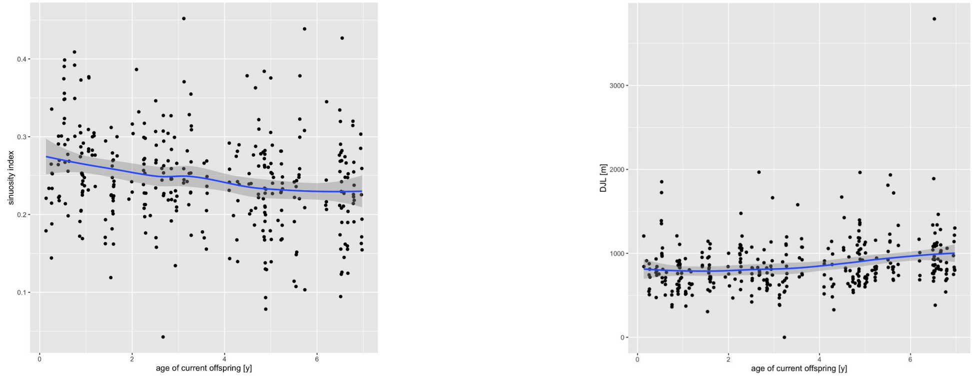
n LMM with the month as an explanatory variable and the year as a random effect showed that month only captured around 2 % of the variance, whereas the full model with the year as a random effect captured around 82 % (LMM, marginal R^2 = 0.021, conditional R^2 = 0.824). When fitting the selected model with the month-year and the focal as random effects, the focal alone explained around 20 % (LMM fruit tree count ˜focal, conditional R^2 = 0.2) of



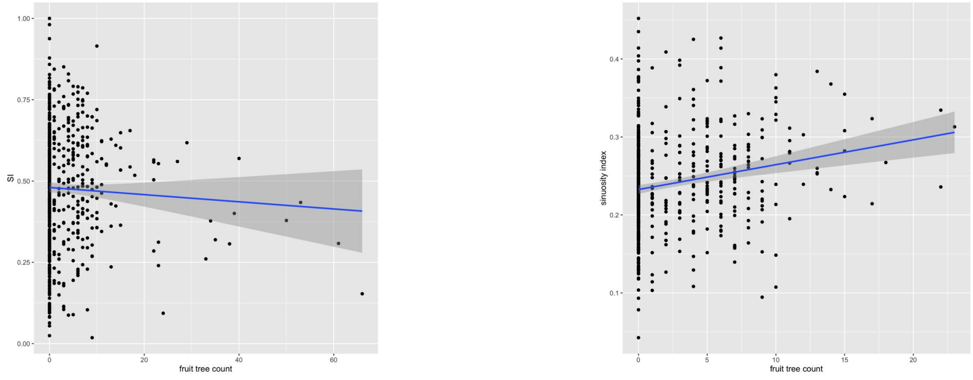
(a) DJL and TDD **(b)** DJL and SI



(c) DJL and sinuosity index **(d)** SI and sinuosity index.



(e) Age of current offspring and sinuosity. **(f)** DJL and age of current offspring.



(g) SI and number of fruit trees. **(h)** Sinuosity and number of fruit trees.

Figure 3.3 – Comparison of movement parameters and some predictors. For the comparison of fruit tree counts with tortuosity, the trees were excluded from the movement trajectories and all variables were recalculated.

Table 3.5 – Statistical models trying to explain fruit trees visited per follow for all age-sex classes and for females with offspring only, respectively.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	Fruit trees visited (all age-sex classes)	(Intercept)	intercept	3.6114	-4.4250 – 11.6477	0.378	-
	n = 610	Day rain	Predictor	-0.005	-0.0213 – 0.0112	0.543	1.009111
	p = 0.0009	Night rain	Predictor	-0.001	-0.0085 – 0.0065	0.795	1.020312
	M-R^2 = 0.051	Average day temp.	Predictor	-0.0353	-0.3121 – 0.2416	0.803	1.020158
	C-R^2 = 0.62	FAI	Predictor	-0.2693	-0.5781 – 0.0396	0.088	1.006977
	Family = Gaussian	ASC: Flanged male	Predictor	-0.0582	-0.7075 – 0.5910	0.86	1.084248
		ASC: Infant	Predictor	0.3942	-1.0489 – 1.8373	0.592	1.008522
		ASC: Independant immature	Predictor	0.39	-0.3259 – 1.1060	0.286	1.069868
		ASC: Unflanged male	Predictor	0.2132	-0.6779 – 1.1043	0.639	1.077087
		SI	Predictor	0.0343	-1.1577 – 1.2263	0.955	1.117046
		Sinuosity	Predictor	9.3123	5.6114 – 13.0132	**<0.001**	1.13266
		Focal	Random	-	-	0.944	-
		Month Year	Random	-	-	**<0.001**	-
b)	Fruit trees visited (only females)	(Intercept)	intercept	0.7262	-10.7477 – 12.2000	0.901	-
	n = 340	Day rain	Predictor	-0.01	-0.0301 – 0.0100	0.327	1.03658
	p <0.0001	Night rain	Predictor	0.0047	-0.0074 – 0.0167	0.446	1.021266
	M-R2 = 0.099	Average day temp.	Predictor	-0.119	-0.5207 – 0.2827	0.561	1.027394
	C-R2 = 0.558	FAI	Predictor	-0.1682	-0.4697 – 0.1333	0.274	1.00783
	Family = Gaussian	Dominance	Predictor	0.6023	-0.2279 – 1.4325	0.155	1.044267
		Age of current offspring	Predictor	0.3906	0.1637 – 0.6175	**0.001**	1.056817
		SI	Predictor	0.644	-0.9861 – 2.2741	0.439	1.107931
		Sinuosity	Predictor	11.7959	6.7263 – 16.8654	**<0.001**	1.114038
		Focal	Random	-	-	**0.006**	-
		Month Year	Random	-	-	**<0.001**	-

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; bold = significance level reached; Statistical variables info's see first table

variation and the month-year combination around 64 % of variation (LMM fruit tree count ˜month-year, conditional $R^2 = 0.64$). Additionally, a rANOVA showed that only the month-year was important in explaining variance and therefore the selected model only kept year as a random effect (rANOVA; Δ $AIC_{\text{year dropped}} = 3224.54$, p <0.001; Δ $AIC_{\text{focal dropped}} = 2986.16$, p = 0.94).

The selected model showed that none of the explanatory variables did explain the variance of the fruit trees visited. Not even the fruit availability index showed an effect on how many trees were visited (Table Table 3.5 and B.2.3). Only the sinuosity parameter partially explained the variance of the fruit trees visited. An increase of sinuosity by 10 % resulted in an increase of around 0.7 fruit trees visited. The model with only sinuosity as an explanatory variable was better than the null model. The total variance explained by the adjusted selected model was 65 %, where only 5 % of it was explained by the sinuosity index (marginal $R^2 = 0.051$, conditional $R^2 = 0.62$).

3.2.5 Path tortuosity between trees and daily movement patterns

Do orangutans show a daily routine?

The movement of orangutans over a day was relatively balanced (Figure 3.4a). As already described in the results of the analysis of DJL, the age-sex classes clearly differ in their distances travelled over a day. Although we have to consider the overall movement pattern, short spikes of higher or lower movements like for infants may be the result of outliers due to a small sample size. This is, for example, the case for infants where we have only smaller sample sizes. The spikes could also indicate a generally higher variation of movement due to playing and learning movement techniques, such as gap crossing (Chappell et al., 2015). Generally, movement activity tends to be stronger right after the start of the follow or after leaving the nest around 6:30, while the morning hours around 9:30 showed the lowest values, which is reflected in all age-sex classes. Overall, unflanged males and independent immatures travelled more during the full day but did not expand their day in the morning or evening clearly to get further. What is noticeable is that many follows showed higher movement during afternoon or early evening hours around 16:00 for unflanged males and independent immatures as well as higher values just after getting up in the morning. The higher movement activity before the end of a follow by young females was also intuitively confirmed by the research staff (Schuppli, personal communication), although the differences still remained low, with an additional 5-7 m per quarter hour. Maybe some fast movements pushed the overall average higher, which results in the intuitive observation of age-sex differences at the end of a follow.

To see if there is a difference between longer or shorter follows in their daily movement footprint, the follows were classified into four categories (Figure 3.4b). Longer follows resulted in higher movement along the full day. There is no specific trend indicating that the dynamic of movement changes at a specific daytime. Although all follows again showed higher activity in the morning, longer distances mostly have arisen from longer distances travelled in the afternoon and during the day, not in the morning. There was also no clear elongation of the day to cover further distances.

Do orangutans show a change in movement when travelling between feeding trees?

The SI and the sinuosity index between feeding trees were analysed. On average, there were 2.2±2.5 GPS points between two trees (n = 2581). The mean distance travelled between trees was 91.5±113.4 m, whereas the mean distance of 112.8±130.4 m from the random subsample was higher. As already described, the same window size was used. The random subsample therefore had the same average number of GPS points between start- and endpoints. A visual comparison of the results did not show a clear difference of movement between trees and any random points.

When further analysing the straightness of movement, the two groups were statistically compared. The straightness index of the random sample and the between-tree movement was compared with a non-parametric Wilcoxon rank sum test. There was no clear difference found between the two groups (WRS, $p = 0.45$).

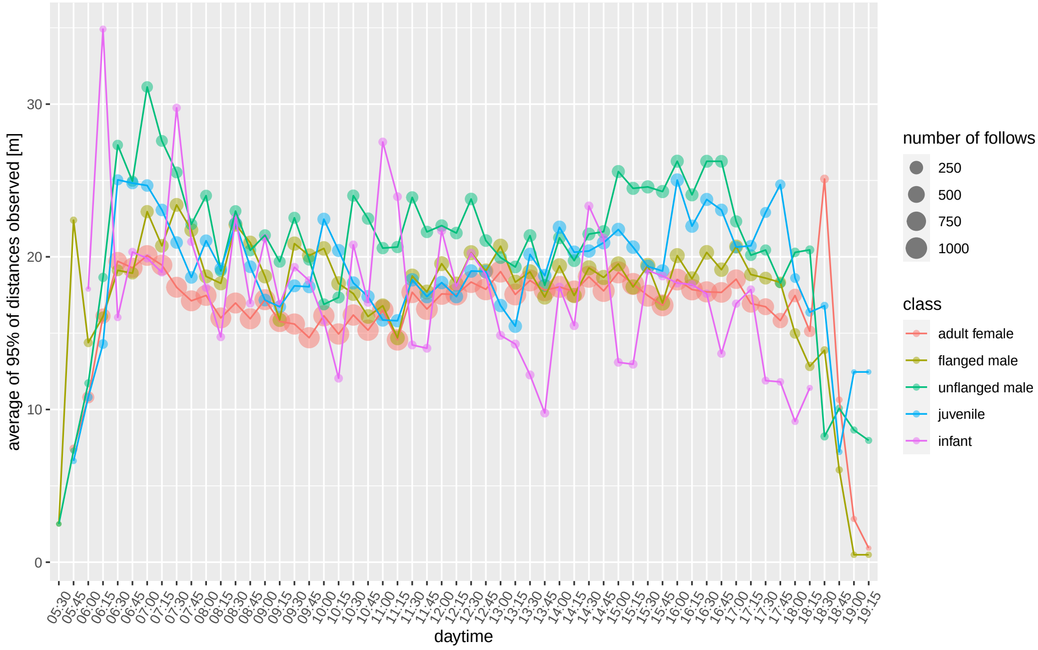
The same was done for the sinuosity, which was calculated in the same way as for the sinuosity section (Equation 3.2). The indication of a difference between the sinuosity was stronger, though not significant (WRS, $p = 0.076$). Sinuosity between two random points tended to be more tortuous than between feeding trees. The measured differences were small and may reflect other influences than internal behaviour. Potentially the environment explains such a difference, for example, the representation of feeding trees. For instance, a random sample might include slightly more movements across minimally more challenging three-dimensional structures. Therefore the spatial arrangement may be less challenging between tree-to-tree movement.

Is the tortuosity of movement between feeding trees explained by external and internal factors?

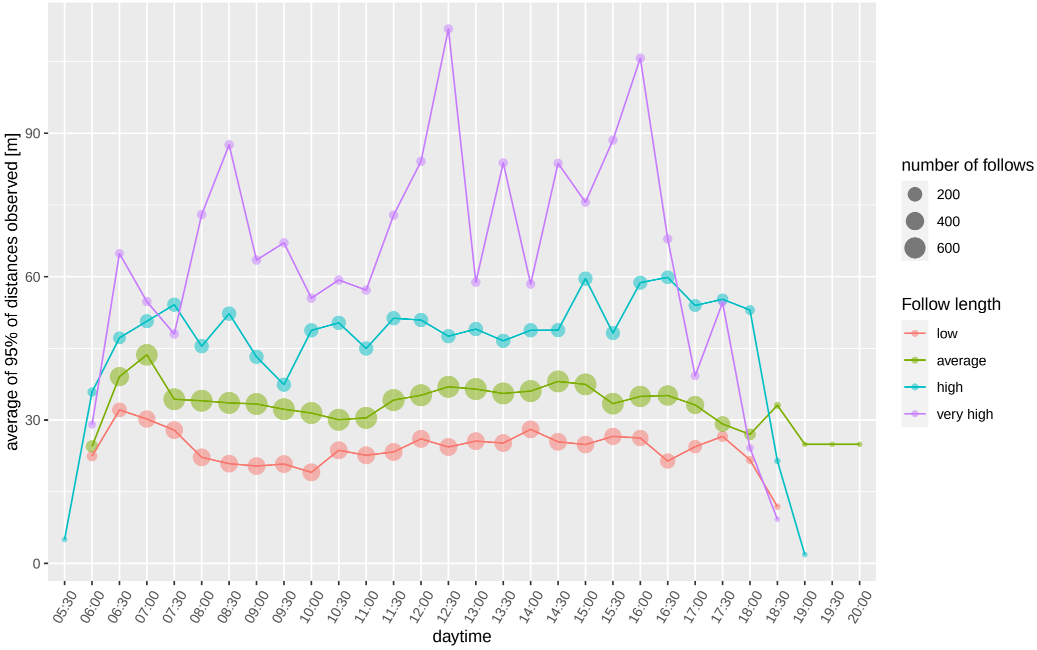
The sinuosity between trees was analysed with an LMM. Of the random effects the date and the sampling window (number of GPS points between) were the strongest random effects. But none of the weather variables (rain, temperature, water level), FAI and age-sex classes did explain the variation of sinuosity between feeding trees (see Table B.3). The fitted model was not better than the null model. An LMM for between-tree-straightness was similarly fitted and checked, but as expected no clear correlations or influences were found.

3.3 Discussion

Generally we can say that our findings for DJL are in accord with Singleton and Van Schaik (2001) (**RQ A.1**). We found average values of 858±323 m for adult females whereas Singleton et al. (2009) states a very similar average and standard deviation of 830±306 m (Table 1.1).



(a)



(b)

Figure 3.4 – Movement over a day analysis (Level 3). **(a)** Average movement per time window of 15 minutes. **(b)** Average movement per 30 minutes for different classes of follow lengths (low <700 m <average <1100 m <high <1700 <very high <10000).

Independent immatures in our analysis, which were mostly females showed an average of 980±336 and in Singleton et al. (2009) 1077±368. Again, the difference is not huge and it could be explained by including male independent immatures. For tortuosity parameter we have no previous findings for Suaq.

3.3.1 Uncertainties in travel distance and tortuosity

How good is the quality of the basic derived movement parameters?

With the calculated movement parameters, we can confirm that the general movement behaviour of orangutans is defined by a low number of quick movements and dynamic changes. The proportion of movement which went missing because of the sampling interval was underestimated. We expected that a sampling interval of 30 minutes is enough to detect small tortuous movement. However, the subsampling of short sampled follows showed that the general movement pattern stays the same (Figure 3.1a).

In contrast to studies describing typical distinct resting movement behaviour and travelling movement behaviour, the steady and slightly tortuous movement depicts the movement of orangutans and is also reflected in the uncertainty analysis (Section 3.1.3). Resting movement is therefore hard to distinguish from normal movement without additional description. Local tortuous movement is probably smoothed out mostly, when a sampling interval of 30 minutes is used. This is also described by Ashbury (2020), who explains that location points were only recorded every half-hour, and the sinuosity of individuals moving and searching for food was not measured. Looking at the defined scales or levels of analysis, Level 3, which corresponds to local, instantaneous movement patterns, cannot really be analysed without looking further into the bias induced by the sampling interval.

For our general analysis on Level 2, the bias is negligible if the results are interpreted carefully. General comparisons between groups like age-sex classes may be more expressive – e.g., if unflanged males move further than flanged males – rather than looking at the direct impact of an explanatory variable – e.g., how much longer is the average DJL of unflanged males than for flanged males. A big advantage of animal focal follows by trained assistants is the qualitative inputs gathered in the field. Any strong tortuous movement which is not be caught by the 30-minutes sampling interval would get the researchers' and research assistants' attention. Rowcliffe et al. (2012) also argues that visual tracking of focal animals could harbour enough information about movement paths to account for such sampling rate bias. Nevertheless, special care has to be given that this information and additional qualitative information is provided to the researchers processing the spatial data sets (in case that field data collection and data processing are carried out by different persons).

The key question is if there are actually behaviourally important short-term movements for orangutans that need to be resolved by the sampling procedure and interval. Because the changes in daily traveled distances are used in many studies this point has to be carefully assessed. The two uncertainties of vertical movement and the sampling bias on DJL have to be taken seriously. Nonetheless, the applied sampling regime of 30 minutes was able to at least reflect parts of the fine-grained movement. This thesis gave a first approximation of how much such a bias occurs for orangutan movements (Sections 3.1.3 and 3.2.1). These results are however based on only a few follows which had a denser sampling rate, which themselves were not 100 % harmonised. Rowcliffe et al. (2012) state a one-minute sampling rate would be needed to reliably estimate the true tortuous movement. I found that their finding tends to also hold for orangutans. The results showed that already the subsampling of every second point of the few follows with dense sampling rate showed that local tortuous movement is missed.

What is the true 'cost‘ of a day journey?

The expressiveness of the 2-D total travelling distance as a movement parameter for orangutans deserves further discussion. Daily traveled distance as a predictor of energy expenditure as a cost should not disregard vertical movement. Thorpe and Crompton (2009) states that vertical climbing is among the most costly positional behaviour. As an arboreal species moving in a three-dimensional environment, this should probably be taken into account. Davies et al. (2017a) describes how important vertical structures are for orangutans and how they can influence their wayfinding. Based on other data sets reviewed for this thesis, the cumulative vertical movement based on the approximation of heights (which is saved in the activity data set as the height in tree) for a follow can be more than 150 m. Thorpe and Crompton (2009) measured the amount of vertical movement during travelling phases and feeding phases and found that vertical descent or climbing accounts for around 15-30 % of locomotive modes.

Suaq, which has a very flat topography, could serve as a prime example for analysing this additional expenditure because the vertical movement does not have to be corrected by the topography. In other sites with strong changes in terrain altitude it may be more difficult to measure the real vertical movement over a follow, because the height is measured as from the base of a tree and not as an absolute value. As we have no information about path altitude yet we can not analyse the impact of it. However, it is important that vertical movement was not observed to differ between age-sex classes or individuals (Isler, 2003; Thorpe and Crompton, 2009). Even more when comparing sites because vertical positional change is in in flat regions less abundant than in more hilly regions. Therefore, our analysis is still valid in terms of comparisons between individuals and follows, with the restriction that the actual influences of explanatory variables have to be taken very cautiously. Such an underestimation of travel distance and energy cost further contributes to the bias of missing out on local tortuous movement behaviour.

3.3.2 Comparison of TDD, DJL, and tortuosity estimators

The DJL is moderately to strongly correlated with the TDD ($r = 0.594^{***}$) (**RQ A.2**). Generally the TDD increased by 0.9 m for every 1 m increase in travel distance (Figure 3.3). DJL and straightness of movement did not correlate with each other, but the sinuosity index and the DJL did. As previously described this is partially the result of the scale dependency of the sinuosity index (Almeida et al., 2010; Benhamou, 2004). To what degree this reflects biological movement behaviour is difficult to distinguish. A quick simulation of the sinuosity function showed that changing step sizes while holding all other variables constant, actually reflected similar exponential behaviour. This is maybe also intended because the index actually compares the actual movement to a correlated random walk model. Thus, we cannot say that longer travel distances actually mean less sinuosity.

When comparing the sinuosity and straightness of movement, it became clear that they both describe different movement patterns of orangutans. They only correlated weakly (linear regression; straightness sinuosity, 607 degrees of freedom, β = -0.09, p <0.001, R-squared=0.07). Mean straightness and mean sinuosity detect movements of orangutans in different ways. To see the differences of movement characteristics for different combinations of sinuosity and straightness, the reader is referred to the Appendix (Figure B.14).

Qualitatively, we can say that the orangutan movement is quite steady and tortuous movement often occurs along the whole trajectory. It looks like the tortuosity of movement is better captured by the sinuosity index of Benhamou (2004), because local tortuous movement is captured along the trajectory. The main critique of the SI by Benhamou (2004) also applies to this data set. The usage of the sinuosity index has the positive effect that it is independent of the DJL parameter. Nonetheless, the SI better captures how directed the total movement of an orangutan is, but does not really reflect how tortuous the trajectory is. Arguably, this is the case because tortuous movement of orangutans is locally bound and much smaller than overall displacement changes of the movement trajectory.

The displacement is also well captured by the TDD and an LMM (not included here) showed very similar results as the LMM of straightness. The only difference found was that TDD correlated slightly with the age of the current offspring, whereas SI did not (LMM of SI Table 3.3). But looking at the scatterplots it was found that this is an effect of interdependencies between the DJL and the TDD, which results in a non-significant linear relationship of age of the current offspring and the SI (Section 3.3.3 and Figure B.15). Because sinuosity, TDD and DJL actually were influenced by the age of the current offspring.

3.3.3 Factors influencing movement

A main goal of this thesis was to determine what factors influence DJL and the tortuosity (**RQ A.3**), from multiple weather variables to FAI, age-sex classes, or the age of the offspring. The fitted models could not find strong influences of the investigated predictor variables and had low explanatory power. Similar variables used in an LMM by Wartmann (2008) for Tuanan found a relatively high explanatory power, which suggests that we have indeed different situations at the two research sites. Especially FAI showed to be a strong influencing factor in Tuanan but also at other sites (Ashbury, 2013; Roth et al., 2020; Wartmann, 2008), while in Suaq FAI appears to be a less constraining factor due to generally very high FAI.

Age-sex classes, age and male dominance

That DJL and sinuosity are higher for younger, less dominant females which can be explained by their developmental exploration phase (Ashbury, 2013). Nulliparous females, which are younger and mostly less dominant, already have been shown to travel further and ranging more (Ashbury, 2013). But for Suaq such differences are not very well reflected by the movement parameters and straightness showed to be higher for more dominant females. Schuppli et al. (2016) give a possible explanation for the lower straightness of younger females. They used the SI as a possible explanation for movement competence, which is worse in younger individuals. The question then remains if the sinuosity wrongly shows higher sinuosity for dominant females because the scale-dependency based on the longer movement distances of younger, less dominant females disguises the effects.

Flanged males and adult females barely differed in the traveled distance per day in Suaq (Table 3.1), in contrast to Tuanan, where differences between age-sex classes were generally much higher and especially flanged males tended to have relatively low DJL of around 670 m (Vogel et al. (2017) in Table 1.1). For adult females Wartmann (2008) and Vogel et al. (2017) found DJLs, which were on average 100 m longer than the DJL of the flanged males. In Suaq flanged males showed even slightly higher values than adult females. Unflanged males had the highest values for DJL in Suaq and also very high values in Tuanan, which were only exceeded by dependent immature females. Although values for dependent immature females in Tuanan differed from Vogel et al. (2017) andAshbury (2020). Overall, DJL was generally slightly higher in Suaq than in Tuanan and adult females, for which the biggest sample size is available, tend to travel 10 % further in Suaq than in Tuanan.

Regarding the differences between age-sex classes in general, two influencing factors influencing can be discussed, namely, the mating strategies and foraging strategies. Hereby, physiological limitations are playing a considerable role in the discrepancy of distances travelled.

FAI is a very important factor controlling the physiological limits of orangutans in Tuanan. Seasonality has shown to influence DJL and TDD, where lower values in FAI negatively impacted the movement in general. In Tuanan flanged males, which are generally bigger and heavier, may have to be more economical, especially when FAI is low. In Suaq, where FAI varies over the year and years but is generally considered very high, flanged males are not so much limited by energy expenditure. Likewise, this explains the relatively higher movement of females and the other age-sex classes. The weaker discrepancy between travelled distance of flanged males to unflanged males in Suaq is, compared to our initial hypothesis, and in comaprison to Tuanan still surprising. The expectation that stable dominance hierarchies between males lead to a bigger difference in DJL for Suaq has to be rejected. The opposite is the case. Flanged males in Suaq tend to travel much longer distances than their counterpart on Borneo and more stable hierarchies are reflected by less difference in travelling distance to unflanged males.

Dunkel et al. (2013) describe a more dominant control of dominant flanged males over sexually active females within their territory. Unflanged males generally tend to compensate their reduced dominance while competing for females by more active searching for females (Section 1.6). Such a searching behaviour results in the longer DJL observed. The difference of the mean travel distance of unflanged males in Tuanan and Suaq may originate from different male-male competition conditions in both locations. Kunz et al. (2021) described that males generally initiate and maintain associations with females. The cost of maintaining such an association is therefore more limited in a less sociable and less productive habitat. Sumatran orangutans accordingly show higher percentages of time spent on feeding (Morrogh-Bernard et al., 2009). Arguably they use the productive environment to strengthen their dominance to monopolise the reproductive access to females Kunz et al. (2021).

Furthermore Dunkel et al. (2013) showed that developmental arrest for males is found more frequently in Suaq than in Tuanan. This is probably the result of longer consortship and female monopolisation of dominant males and therefore intensifies the risk of becoming a flanged male when not being able to gain dominance in an area against other flanged males (Atmoko et al., 2009; Dunkel et al., 2013). Therefore, we can argue that unflanged males have to invest even more into searching in Suaq than in Tuanan, which is further contributing to the overall longer DJL. With respect to these variations in estimation of the different cited studies for Tuanan and the above executed uncertainty analysis we can safely conclude that the travel distance for flanged males is more limited in Tuanan than in Suaq and that the observed more stable dominance hierarchy in Suaq is probably maintained by longer DJL Dunkel et al. (2013).

We can further analyse the movement on Level 3. As discussed in Section 3.3.1, results on this level have to be taken with caution because the sampling regime may miss fine-grained movement patterns. Generally we cannot observe much differences of movement during daytime 3.4a. Possible effects where unflanged males prolong their daytime to search for females when adult females and flanged males are resting were not observed. But a weak trend of higher activity levels of independent immatures (mostly juvenile females) coincided with higher activity levels of unflanged males in the beginning of the follows and towards the end of follows. This may reflect that successful mating of unflanged males with sexually active females does occur mostly with nulliparous females, which are more active at the same time (Atmoko et al., 2009). Future work could look into whether such activity over daytime is similar or dissimilar in Tuanan. Flanged males in Tuanan, which clearly travel less, may show less movement at the end of follows or they similarly move less over the whole duration of follows, as we we found in Suaq. In Tuanan, flanged males clearly have shorter active periods compared to unflanged males (Vogel et al., 2017). Such a difference could induce age-sex specific differences in movement during daytime. In Suaq, where follow durations are not significantly different, such patterns are nearly absent as described above.

Concluding the discussion of the differences between age-sex classes there is almost always enough fruit available in Suaq and therefore the average DJL is higher over all follows and for all age-sex classes compared to Tuanan (sit and wait vs. search and find). Further differences originate from different reproductive strategies. Especially, males adjust their mating and movement strategy based on the habitat productivity and social conditions. Arguably, their is a reaction of temporal activity during the day based on such reproductive strategies for unflanged males and nulliparous females.

Tortuosity of movement and feeding trees

The age and dominance of females did not clearly influence the movement behaviour of adult female orangutans. What we can see is that the trends showed a difference of the lowest dominance category and therefore the youngest females. Their corresponding DJL was longer and rather resembled the movement pattern of independent immatures. If there is an actual difference between older females of higher age and higher dominance remains unclear. None of the LMMs showed a clear relationship.

We found a statistically significant difference of age-sex classes for the SI and sinuosity, but when corrected for random effects like months and year, these differences disappeared. Our hypothesis of a clear difference between age-sex classes can therefore be rejected (**RQ A.3**). This is in agreement with Alavi (2018) who also did not find a difference in tortuosity between males and females in Tuanan.

Comparing the found SI for adult females with the results of Wartmann (2008) showed nearly no difference (Tuanan = 0.47, Suaq = 0.46±0.18). This is contradicting results from Schuppli et al. (2016), who found clear differences when comparing the straightness of movement. At least the trend of slightly higher tortuosity in Suaq remains. However, no influence of dominance or age on the tortuosity of movement within the Suaq research site is in agreement with Schuppli et al. (2016). A central problem posed by the research question (**RQ B.2**) raised by us and also by Schuppli et al. (2016) to use the SI for range competence is the strong sampling bias that we have revealed in the subsampling analysis (Section 3.1.3). I argue that general trends are visible and therefore results are not fully contradicting but a very clear interpretation of the SI or rambling ratio (in Schuppli et al. (2016), which is reciprocal to the SI), remains difficult. This is mainly due to the sampling interval of 30 minutes, which misses a significant portion of local tortuous movement. Notwithstanding the additional validation by researchers in the field may show that such local tortuous movement is less important in explaining range competence and that we actually can capture ranging competence by a 30-minute sampling interval. But for Suaq the number of fruit trees visited for all follows often correlated with less straight movements and higher sinuosity. Furthermore, our results relating to age-sex classes are contradicting as well and do not really help to explain if SI can be used as a proxy for range competence, because the infants showed very high straightness. However, this result may be more influenced by the very young infants, which are often still clinging to their mother. Independent immatures, on the other hand, showed low straightness, which would fit in with the idea of having less ranging competence. The sinuosity index as a second indicator is not helping either because infants showed higher sinuosity, whereas independent immatures showed lower values, probably due to their longer day journeys and the scale dependency of the sinuosity index. I therefore argue that the higher amount of feeding possibilities in Suaq may result in the slightly additional tortuosity, whereas feeding competence plays a minor role.

The previously expected higher clustering of feeding possibilities in Suaq and the higher amount of ranging in between are also contradicting the results of the generally more tortuous movement in Suaq. Initially, we assumed more directional movement between tree patches. Singleton et al. (2009) observes that female orangutans do not travel further in more heterogeneous habitats because they reach all resources within their normal day journey and therefore we assumed that they optimise their routes. Longer and more direct travelling between feeding trees with subsequent local tortuous movement when a patch of feeding trees are reached should have been detected by the analysis in Section 3.1.4. However, no clear difference between the SI of a random comparable samples and the movement between trees was found. On the level of the 30-minute sampling interval the movement between patches of fruit trees led to minimally higher tortuosity, perhaps owing to stronger foraging and searching behaviour in between tree patches. Therefore, the higher patchiness of feeding trees in Suaq actually might lead to higher tortuosity, which would be in agreement with the findings presented in Section 3.2.3 and Schuppli et al. (2016). Fruit trees were also explained by DJL. Due to the weak strength of the correlation, however, we do not know the direction of the relation. Maybe the length of the DJL influences the number of fruit trees because longer travel distance means more feeding opportunities, assuming that the feeding sources are uniformly distributed. Alternatively, opportunities of feeding at a feeding tree may have a positive effect on the possibility of travelling further than usual. Nonetheless, DJL and the derived SI had a strong positive correlation with fruit trees visited. I tend to conclude that a longer day journey intrinsically predicts a higher number of feeding trees because the correlation is very high and the effect in the other direction would be minimal. The mapping of feeding possibilities in Tuanan and Suaq with the same methodology could shed light on the actual distribution of resources and the alteration of movement, based on these resources.

Fruit availability

In Suaq monthly changes of DJL do occur very often. Interestingly they do not seem to be directly linked to FAI or weather (Figure B.13), however. There may be some unknown or unclear variation pattern of fruit availability. The big difference between years may show such a variation. The unexpected clear difference of rainy season in Suaq at the end of the year did not end in explaining variations between months compared to many other sites like Tuanan. Furthermore, the results of including ENSO indices to explain FAI were not conclusive. No movement parameter was clearly influenced by the FAI. Fruit availability patterns in Suaq may be more difficult to observe and to capture because clear seasons of fruiting are absent. Strong variations of FAI even indicate that FAI is probably influenced by the sampling method of GPS points. Because a clear description on how the data is standardised is missing we cannot elaborate further on the possible sampling biases. However, we can guess that objectively estimating the amount of ripe fruits for a tree is already difficult. Hence, being able to estimate the real fruiting amount based on a random sample of trees may further obscure clear, reliable results. A full mapping of feeding trees which would facilitate the easier approximation of FAI has not yet been done (Schuppli, personal communication). Therefore, the more fluctuating patterns of fruit availability may not show specific trends or current changes very well.

Nonetheless, the analysis showed that the available FAI even showed a negative correlation with DJL, although the effect was statistically not significant. A clear sit-and-wait strategy during lower FAI can definitely be rejected ,and as proposed by Morrogh-Bernard et al. (2009) a search-and-find strategy is observed. The slightly negative trend of FAI on DJL may suggest that orangutans in Suaq have the availability to invest in other activities than foraging, such as reproduction when FAI is high. Also, they do not adjust activity or movement based on the available fruit but are more driven by internal factors, such as the age of the current offspring. Conversely, Morrogh-Bernard et al. (2009) showed that fruit availability had an effect on the start time of activity of Sumatran orangutans in Ketambe. This has not been observed for the data analysed in this thesis. Whether FAI influences daily movement therefore appears to be not only species-specific but to a higher degree site-specific.

Weather variables

Weather variables of Suaq did not explain the movement parameters and did not explain FAI. Even high precipitation did not result in changes of movement. The positive tendency of day rain and temperature on DJL was not expected. The negative impact of night rain may be explained by the shortening of activity if orangutans react with later activity. Such a change of daily activity has already been described by Parsons (1999). The question remains why day rain then does not show the same pattern. Possibly, the orangutans compensate for short stops during heavy rain events or day rain is more strongly associated with months where other ecological factors favor longer DJL. The observed pattern in Tuanan that speed, directness and distance travelled was higher with lower rainfall could not be confirmed by our methodology. One of the main reasons why altering movement patterns are not correlated with rain data sets may be explained by the lack of meaningful information of pooled 24-hour rain data sets (Isbell 1983 in Parsons (1999)). Such a pooling may obscure the clear impact of rain on movement. The inclusion of temporally more densely sampled weather data, possibly based on field observations by research assistants, may help to fill this gap.

Higher temperatures do not seem to hinder orangutans from travelling further to avoid overheating or being physiologically stressed. For other primates such a pattern was shown. McLester et al. (2019) analysed red-tailed monkeys at two sites of different climate (*Cercopithecus ascanius*) and found that hourly travelled distance and daily travelled distance both were negatively impacted by higher temperatures but not by higher precipitation. The climatic habitat of orangutans may be very stable and therefore the impact of daily weather does not alter the movement pattern of orangutans.

Generally, we can conclude that although there are different weather phases and statistically significant different temperature and precipitation periods, this has nearly no influence on the movement on Levels 1 and 2. Field observations of behavioural changes to rain and resulting changes in movement are probably bound to the third level, the highest temporal resolution.

Chapter 4

Analysis II: Ranging behaviour

(Level 1)

4.1 Methodology

4.1.1 Definition

Home range

The concept of animal home ranges was introduced in 1943 by Wiliam Henry Burt. It essentially describes spatial and temporal observations of animals on a map and aims to show the distribution of an individual (Burt, 1943). In biology and ecology, the concept of home ranges is widely debated. It often remains unclear what exactly the home range means. We do not know the exact ecological relevance of the home range or how exact such a delineation is with the above-mentioned definition. So it is important to know what the ecological reasons for such a spatial distribution is. In terms of orangutans we can say that the spatial distribution of resources especially feeding trees, density of food, sex related distribution strategies (as already mentioned female philopatry and male dispersal), inter (reproduction) and intrasex (competition, hierarchies) related interactions best explain the space of action of an orangutan (Ashbury et al., 2020; Singleton and Van Schaik, 2001; van Noordwijk et al., 2012). To a lesser degree also some hurdles and spatial limitations are set. Powell and Mitchell (2012b) proposes that the best concept of a home range is the cognitive map of the environment of an animal that it chooses to keep. Nonetheless to know what cognitive map orangutans have

of their environment needs much more studies and therefore are home ranges mostly derived by the distribution of their sampled spatial positions via GPS-samples, telemetry or camera traps. This brings up further questions which are widely debated. What is the best method to delineate a home range by the available positions of an individual?, What percentage of the delineated space should be included, do occasional excursions count as well? Furthermore a big problem poses the delineation in time instead of space. A solution that incorporates parts of the problem of spatial delineation is the usage of spatial occurrence or so called probability distributions which incorporates areas with higher use and areas with lower use (Katajisto and Moilanen, 2006). But again if the importance of an area for an animal is also clearly reflected by higher occurrence probabilities is debated (Powell and Mitchell, 2012b). Some species tend to satisfy their needs of an area in a very short time. A perfect example for such quick spatial needs in rain forests would be natural mineral licks which are even observed to be occasionally used by Bornean orangutans (Ampeng et al., 2016; Powell and Mitchell, 2012b).
In this thesis, four methods were used to retrieve a home range by GPS-locations which increase in complexity. First home range boundaries, second probability distributions (and boundaries derived from them), and third probability distributions that even include a temporal dimension or delineation. Additionally, the research period was also manually separated into different research periods.

In the meta-study by Singleton et al. (2009) - one of the fundamental published studies for developing the concept of this master's thesis - the distribution ranges of female orangutans were compared at different sites. Almost all studies used MCP to estimate the size of the home range. A species-specific difference in home range size for female orangutans was found. *Pongo abelii* had the largest and *pongo pygmaus morio* the smallest home range sizes (*pongo abelii* >*pongo wurmbii* >*pongo pygmaus morio*). Habitat properties were described as having an impact on home range sizes too. E.g. range sizes of 1.5 km^2 to 4 km^2 in Ketambe (Habitat type: Dry lowland, alluvial, submontane with homogenous habitat mosaic) were observed and range sizes >8.5 km^2 were found in Suaq (peat swamp forest). Bigger home ranges in Suaq may be explained by the combination of five different habitat types, coastal peat swamp, transitional swamp, back swamp, riverine and hill and therefore more movement between those areas (Russon et al., 2009; Singleton et al., 2009). Additionally, a higher clumped distribution of fruiting trees in the peat swamp forest may lead to more scramble competition between orangutans (Knott et al., 2008; Singleton and Van Schaik, 2001).

In terms of methodology, the meta-study identifies three main sources of error for estimating home ranges. First, the algorithm used to compute the home ranges, second, the size of the study area, third, and most importantly, the temporal resolution of the GPS data and the duration of the study for individuals. Singleton et al. (2009) state that a longer observation period leads to larger home ranges.

Core range

Core area is a relatively arbitrary concept to define an area where the animal spends most of its time. One of the various definitions attempts to define core range as the area that an animal knows well and where its mental map and spatial representation is very clear. For species with stationary home ranges, which is expected in female orangutans, core ranges should exclude infrequent excursions out of the known spatial range (Singleton and Van Schaik, 2001). For simplicity, many studies use a rather arbitrary threshold of 50% of the original home range (Ashbury, 2013; Knott et al., 2008; Singleton and Van Schaik, 2001; van Noordwijk et al., 2012; Wartmann et al., 2010). Either by cutting off 50% of the points or by reaching the 50% threshold of a utilisation distribution. Knott et al. (2008), analysed female competition within core areas and found that resident females usually dominate a competitions. However, a precise biological or ecological definition of orangutan core territories was missing (Knott et al., 2008). For orangutans, I would argue that the threshold of 50% is too low to meet the definition above because excursions are rare. Nevertheless, such core areas show the most temporally important areas for an orangutan. Since many other studies have used this threshold, it was done for this thesis likewise. Overall, a definition of core areas and information on the importance of spatial requirements for orangutans in general would be appreciated. Singleton and Van Schaik (2001) found core areas for orangutans in Suaq, where they averaged 49% of home range size. Rare excursions were successfully excluded by cutting off 50% of points starting from the centroid.

4.1.2 Workflow

An analysis of the ranging behaviour was conducted for the ten most followed females (overview of selected individuals Table C.1). The four most frequent followed females, Lisa, Friska, Ellie and Cissy accounted for roughly 40% of the total data (407 follows) and roughly 80% of the data of the selected females (Figure 2.3). For the analysis of ranges, all points were included not only NN-follows (Figure 2.2). Additionally, some data was generated by creating new GPS-points or partial follows, when other orangutans met the followed individual. This is a so-called party and is remarked in the GPS and the behavioural data in field. A party point is defined as when a dependant orangutan comes nearer as 50 m of the followed individual. On the contrary to the paper of Wartmann et al. (2010) morning points were included in the analysis, although they may be sometimes duplicated due to subsequent follows over a few days. However, leaving them away may also delete information. Additionally, morning nests may reflect spatially more relevant areas for orangutans. Therefore, leaving them in the data slightly gives importance to them. Party points of dependant focals were additionally added to the data set. No spatial limits or boundaries were set like the river or other regions off-limits. Forest structure or spatial canopy variations could not be included because it would need considerable research effort to retrieve some useful data to include. After preparing the full data set, the spatial autocorrelation of occurrences for individuals was calculated. For delineating the home ranges the data was split into four partial research periods (Section 2.2.1) and the total period was added as the 5$^{\text{th}}$ period. This results in two scopes of temporal resolution. For every partial research period and the full follow duration the home range was calculated for every of the ten most followed females. It was calculated with different home range estimators where every home range estimator has a different parametrisation (Details see Section 4.1.4). For all HRE or derived quality indicators which rely on a reference grid, a grid was defined over the research area with a resolution of 25 m which compromises calculation duration and resolution. For all individuals at minimum the core range which considers 50% of GPS-points and the home range of 95% of the GPS-Points was derived and saved. The percentage either relates to the amount of GPS-points considered for the calculation of a range. It is derived by the Cartesian distance of the centroid of all points (for MCP). Or it relates to the threshold of a volume of the UD (for KDE, BRB, AKDE).

The HRE and the home range parametrisation was then evaluated by different home range descriptors (Section 4.1.9). After the evaluation of the parametrisation and the different HRE the number of feeding trees per home range was derived. Additionally, possible other explanatory variables were added to the data. For the ten females, it was analysed how the age category (arbitrary categories 1-5), matriline (relatedness, matriline groups) and the dominance category (1-4) influence the area of their home ranges.

Calculation of overlaps

After analysing the home ranges, the same was done for overlaps. The overlaps were always calculated between the same corresponding data threshold (core range, home range) and the same used parameters and algorithms. However, there are again various types of overlap algorithms. Below are some examples how overlap can be measured. For this thesis, the following overlap indices were calculated, but only some of them are used in the following analysis:

- Total **area shared** with others in percentage of own HR. This is the only overlap indicator which is independent and does not show an interaction between two individuals.

$$\frac{(A \cap B) + (A \cap C) + ...}{(A)} \tag{4.1}$$

- The dyadic **relative overlap**. Which is the HR shared with another individual in percent of the own HR. This is the only directed overlap index used, all the others are undirected. This means that the value is not the same if calculated for either one of the currently analysed dyadic focals. To overcome redundancy, the dyadic value was saved as a second overlap index, the relative overlap where the individual A is part of the individual B's HR.

$$\text{relative overlap} = \frac{(A \cap B)}{(A)} \text{ or relative part of} = \frac{(B \cap A)}{(B)} \tag{4.2}$$

- The **Jaccard overlap** which compares the overlap to both HR-sizes and therefore stays the same for both individuals (Jaccard, 1902).

$$\frac{(A \cap B)}{(A \cup B)} \tag{4.3}$$

The following overlap indices are only calculated for the KDE and BRB algorithms because the utilisation (probability) distributions of the home ranges were used. This is a big advantage because the temporal and spatial density of overlaps is taken into account. The following overlaps were calculated with the adhabitatHR package (0.4.19).

- **Utilization Distribution Overlap Index (UDOI)** of Fieberg and Kochanny (2005) which is a measure of space use sharing. According to the author, this algorithm gives the most reliable results.
- The **Bhattacharyya Affinity (BA)** was also proposed by Fieberg and Kochanny (2005) and describes the overall similarity between two UDs (Clapp and Beck, 2015). Values go from 0 (no overlap) to 1 (identical probability distribution).
- The **Volume of Intersection (VI)** which is simply the volume of intersection of two UDs. It often correlates highly with the BA (Clapp and Beck, 2015).

For all derived overlaps, the number of fruit trees was derived as well. Influencing variables were then analysed using a LMM. The explanatory variables used were relatedness (matriline), age category and dominance. Additionally, it was analysed if these variables do explain partially the variance of fruit trees in the overlaps. Finally, a discussion was done by comparing the results to other sites and discussing the methods used.

Normalisation of fruit trees

Feeding trees were sampled when an orangutan stays longer than 5 minutes in a tree and is eating the fruits of it. This data set was used to retrieve the number of such tree points per home range or overlap. However, sampling points of trees can be redundant when a tree is sampled many times by different follows. Our main interest belongs to the location of potential feeding sites. However, without clustering or defining such feeding sites, we had to normalise the number of fruit trees in an area. Because initially, the variation of fruit tree in an area was mainly influenced by the amount of follows conducted in an area and the size of an area. To reach a normalisation of the number of fruit trees, there was only one simple method without digging into analysing and researching the research effort in the research area. The number of fruit trees were compared to the total number of GPS-Points sampled. Therefore, for every HR or every overlap, the number of fruit trees was divided by the total number of GPS-Points including the number of fruit trees. The normalised tree value reflects the number of trees sampled in an area compared to the total number of points taken.

4.1.3 Spatial autocorrelation

A long discussed problem of animal movement data is spatial autocorrelation. Nearly every data set of animal tracking data is spatially autocorrelated to some degree (Dray et al., 2010). This poses a problem for movement ecologists because many movement indicators assume statistical independence (e.g. home range estimators like kernel distance estimation). In simulations higher spatial autocorrelation showed a underestimation of home range sizes (Calabrese et al., 2021; Swihart and Slade, 1985b). The movement ecology of an animal and the sampling interval mainly influences how big the spatial autocorrelation is Dray et al. (2010); Swihart and Slade (1985a). Lower sampling intervals increases the possible distance travelled by an animal and therefore increases correlation between two subsequent fixes. The spatial correlation decreases with time and a method could be to subsample a data set to get higher time intervals and lower spatial autocorrelation. But finding the time when GPS-fixes are independent is not trivial and probably not even helpful. Rooney et al. (1998) for example, did not even find independence of fixes when subsampling the tracking points with a sampling interval of a week. While subsampling did not reduce spatial autocorrelation important information of home range use was lost during the subsampling process and home ranges were highly underestimated (Fortin and Dale, 2009; Rooney et al., 1998). Even though the study looked at hares and voles which may differ strongly to primates, a lose of biologically relevant information of space use can be expected for primates and more specific for orangutans too. Rooney et al. (1998) further states that to overcome spatial autocorrelation biases in home range estimations it would be best to have a long-term study with a very coarse sampling interval (Rooney et al., 1998). This means a high continuity and a fine scale sampling interval would reveal any biases, although the data itself would be highly spatially correlated.

Generally spatial autocorrelation bias in home range analysis is considered as a statistical problem in statistical movement ecology but with less biological meaning. On the contrary, spatial autocorrelation may be even desired to describe different use of space, for example to compare different habitats for a species (Rooney et al., 1998). Many authors argue that spatial autocorrelation is an inherent feature of animal tracking data and that much information is lost if we try to reduce it. Nonetheless some statistical home range estimators are more affected than others because they assume statistical independence between relocations (like classical KDE algorithms) (De Solla et al., 1999; Fortin and Dale, 2009; Rooney et al., 1998). Communicating spatial autocorrelation and discussing potential impacts is important and even adds biological relevant insights. Observed impacts in simulations showed mostly a decrease in home range size with highly autocorrelated data. A major advantage in orangutan studies may be the research method of focal animal follows. Any biases due to sampling intervals and spatial autocorrelation can be judged by the researchers and researcher assistants who are working in situ. This is not so much the case for GPS collars in many other animal movement ecology research. Wartmann (2008) executed an analysis of spatial autocorrelation and looked at the influence of autocorrelation on home range estimates (KDE). She found bigger home ranges with higher autocorrelated data, but the differences between home ranges were statistically not significant. Even when using only night nests instead of all GPS data points, spatial autocorrelation was present. Therefore, this thesis renounces to reduce spatial autocorrelation by only using night nest points at the risk that there might be a slight influence on the resulting home range sizes. The main reason is that a reduction of points always means a loss of biological relevant information.

Nonetheless, temporal autocorrelation was measured by using the Schoener's ratio (t^2/r^2) implemented in the R package adehabitatHR and some customised function (Calenge, 2006b). Where t^2 describes the mean squared distance between two successive GPS fixes and r^2 describes the mean squared distance between each GPS-Point and the centre of all GPS-points. Values of Schoener's Index above 2 are indicating negative spatial autocorrelation and values below 2 indicate positive spatial autocorrelation (Swihart and Slade, 1985b). We see that the Schoener's I for all individuals are comparable and that all data is strongly autocorrelated. However, orangutans (esp. Lisa, Friska), which have few follows at a denser sampling rate (follows in early 2011 of 5 min sampling interval), do not clearly show higher spatial autocorrelation. We conclude that different focals home ranges are comparable and spatial autoccorelation may be a problem, but to solve it would be at the cost of loosing more valuable information. Most importantly, the quality of our results are much more dependant on the sampling frequency and the study duration.

Table 4.1 – Overview of Schoeners ratio.

orangutan	t^2/r^2
Cissy	0.014
Ellie	0.021
Friska	0.017
Lilly	0.02
Lisa	0.017
Raffi	0.013
Sarabi	0.011
Tiara	0.016
Trident	0.034
Yulia	0.048

4.1.4 Selected home range estimators

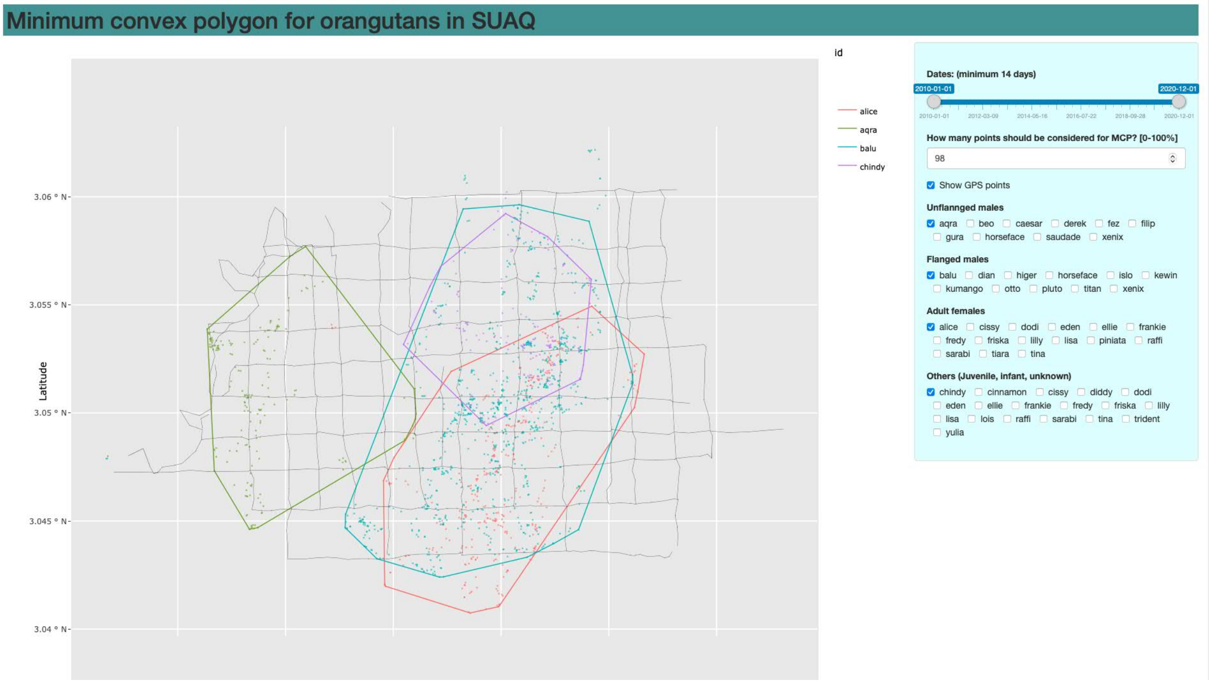
The quality of Home Range Estimator (HRE) is difficult to access. Which of the estimators is best for a given species or data set is hard to distinguish (Horne et al., 2007; Powell and Mitchell, 2012b; Walter et al., 2015). To evaluate the performance of the estimators, simulations or validation would be needed (Walter et al., 2015). The true home range as a quality control is not known for any of the followed individuals. This is a standard problem for the selection of a single best home range estimator. Therefore this thesis uses multiple HRE of different generations and compares them with the presented data set. Gregory (2017) state e.g. that using multiple algorithms and discussing them is the best approach to accomplish expressiveness because even first generation algorithms in a case of primate studies about chacma baboons (*Papio ursinus*) outperform more advanced algorithms. The comparison allows us to still get behavioural insights because the same method was used for every given individual. The variation of algorithms on the other hand gives us further information about how expressive the presented results are and how different HREs influence the findings. The findings then can be further compared to other research findings and their home range delineation methods 1.1. For this thesis three main HREs were used. A first generation home range estimator is the MCP, a more advanced second generation estimator, which makes use of the probability of occurrence is the KDE (Fleming et al., 2016; Powell and Mitchell, 2012a; Worton, 1989). The third estimator was BRB which even incorporates a temporal dimension and is a third generation estimator (Byrne et al., 2014; Kranstauber et al., 2012; Walter et al., 2015). A fourth mathematically very complex method from the shiny web interface by the authors of the ctmm package in R was used for only the full study period (Calabrese et al., 2016; Fleming et al., 2016). Specifically it uses AKDE for delineating a home range. The web interface was used because in R some functions did not work.

Initially, the estimation of home ranges by a time local convex hull was done as well. The algorithm is related to the MCP method and does not give a probability distribution (Walter et al., 2015). But because every home range calculated had to be evaluated to adjust parameters, the use of this algorithm was omitted.

4.1.5 Minimum convex polygon

A Minimum Convex Polygon (MCP) or simply a convex hull was one of the first methods used to define an animal's home range and was and sometimes still is very common (Downs and Horner, 2008). Common because it is a first generation and very simple algorithm. Of the seven cited sources estimating home ranges for orangutans five used MCP for estimating home ranges (Table 1.1). A main advantage is also that this algorithm is non-parametric and hence comparable between studies (Huck et al., 2008). MCP's are generally considered to be very unreliable because they are sensitive to sample size and outliers, do not provide information on internal space use, and are less useful if the home range is not inherently convex (Downs and Horner, 2008; Worton, 1989).

The MCP is derived from the minimum convex polygon which encloses all points sampled. Per definition, the angle of three points which are connecting the hull around the home range must be lower than 180 degrees. Examples and results of this method can be seen on the shiny app created for this thesis. The goal was to find the first results for the concept presentation of this thesis (Figure 4.1).



Dates: (minimum 14 days)
2010-01-01 – 2020-12-01

How many points should be considered for MCP? [0-100%]
98

☑ Show GPS points

Unflannged males
☑ aqra ☐ beo ☐ caesar ☐ derek ☐ fez ☐ filip ☐ gura ☐ horseface ☐ saudade ☐ xenix

Flanged males
☑ balu ☐ dian ☐ higer ☐ horseface ☐ islo ☐ kewin ☐ kumango ☐ otto ☐ pluto ☐ titan ☐ xenix

Adult females
☑ alice ☐ cissy ☐ dodi ☐ eden ☐ ellie ☐ frankie ☐ fredy ☐ friska ☐ lilly ☐ lisa ☐ piniata ☐ raffi ☐ sarabi ☐ tiara ☐ tina

Others (Juvenile, infant, unknown)
☑ chindy ☐ cinnamon ☐ cissy ☐ diddy ☐ dodi ☐ eden ☐ ellie ☐ frankie ☐ fredy ☐ friska ☐ lilly ☐ lisa ☐ lois ☐ raffi ☐ sarabi ☐ tina ☐ trident ☐ yulia

Figure 4.1 – Enclosing of GPS-Points by a convex hull by the MCP-algorithm. Normally only 95% of the points are considered (cutting the 5% furthest away from the centroid of the points) to avoid outliers which have a huge impact on this algorithm. Example above is a MCP from the "orangapp" constructed as a preparation to this thesis where the cut off value for points was chosen to be 98% because outliers are rare.

4.1.6 Kernel density estimation

Theory

The following algorithm reminds us a bit of the grid cell method, which was historically probably one of the first methods to measure the spatial distribution of an animal and was also often used in orangutan studies (Table 1.1. Grid cell method means that the number of points/sightings per cell of a predefined grid is counted and the area of all cells is summed up for the total range size or the number of points per grid is visualised which results in a heat map (Haugen, 1942). In orangutan studies this grid was often around 100-200 m.

The Kernel Distance Estimation (KDE) is a second generation algorithm which calculates a utilisation distribution (= probability or occurrence distribution) which uses probability functions (i.e. the probability function adapts to the data), so-called kernel methods for estimating the spatial likelihood of occurrence over time (defined by the data set) for a specific individual. However, also this method comes with flaws (Worton, 1989). KDE is mathematically still relatively simple and is applied in many fields. Just think about heat maps calculated with KDE for example for analysing the action spaces of individual players on the field or analysing crime occurrences. The broad application also led to many adjustments, improvements and variations of the KDE (Fleming et al., 2016).

The KDE is still a non-parametric home range estimator. It is often wrongly assumed that, this means that KDE does not need parameters. With non parametric and parametric the underlying statistics of a home range estimator is meant. Non-parametric – like the KDE algorithm – means, that the algorithm does not presume an underlying distribution or model structure. However, in this thesis, we will also talk about the parameters or the parametrisation of an algorithm, which does not mean that an algorithm is non-parametric or parametric.

To calculate the UD we basically sum up multiple density distributions. The bivariate probability density function is derived from the given locations of the animal (Seaman and Powell, 1996; Worton, 1989). With the resulting UD we can describe the intensity of space usage at any given location for an animal. For delineating home ranges from a UD the volume of the wanted outline can be defined. For example if we want the 95% delineation from any given UD the volume starting from the highest density is measured until 95% of the volume is reached (From the top to the bottom/ground in the graphic below). At this threshold the binary delineation is then projected on the two dimensional plane (Seaman and Powell, 1996).

$$\widehat{UD_x} = \frac{1}{nh}\sum_{i=1}^{n} K(\frac{x - X_1}{h})) \tag{4.4}$$

Variables: x = any given position, n = number of GPS-fixes, h = bandwidth, K = kernel function, X_i are the coordinates at the i^{th} GPS-fix. KDE developed by Worton (1989) with its result the UD which estimates the probability at any given space in the two dimensional space (here only one dimensional).

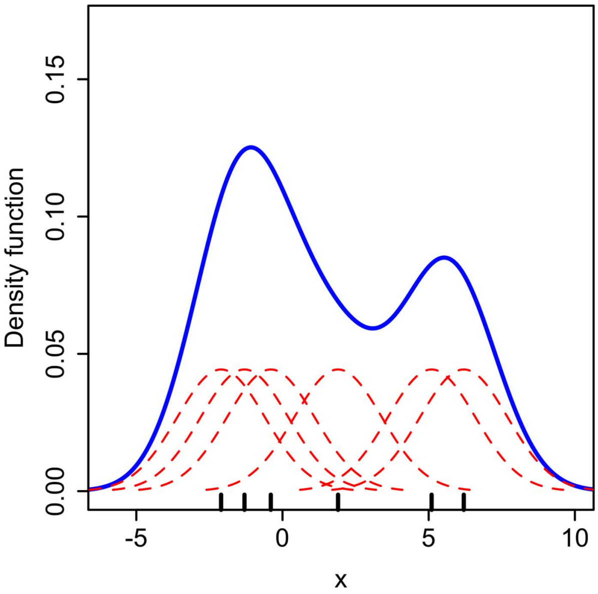


Figure 4.2 – Schematic KDE calculation by summing up multiple density distributions to one utilisation distribution. The underlying density function uses parameters which can influence the results immensely. Image from Commons (2020).

The KDE uses two main parameters which have to be given to the function. The most important parameter is the bandwidth h (Downs and Horner, 2008). The bandwidth represents how intensively the fixes are contributing to the density functions (in Figure 4.2 red) depending on the distance to the current i^{th} point where the density function is calculated. Small bandwidths mean the results are very grainy because only very near points or at its maximum no other point nearby is considered for the local kernel (density function). This means that small scale patterns are visible but with increasing number of breaks between probability maxima. Big values mean a very smoothed surface which can lead to oversmoothing where areas of no occurrences are showing high values because of fixes which are lying far away (Downs and Horner, 2008; Seaman and Powell, 1996).

The bandwidth can be estimated with various methods using the given distribution of data or it can be approximated and then adjusted manually. The default method in the adehabitatHR package is the reference bandwidth (REF). Hereby, the bandwidth is derived from the standard deviation of the distances of the GPS-fixes which are assumed to follow a normal distribution. In real data, this is mostly not the case and the assumption is not helpful to estimate reasonable home range sizes. It mostly oversmooths the occurrence distribution (Seaman and Powell, 1996). The Biased Cross-Validation (BCV) and Smoothed

Cross-Validation (SCV) are belonging to the category of cross-validation techniques which were introduced because the traditionally used LCSV tended to undersmooth the data (Heidenreich et al., 2013; Rodgers et al., 2007). The fourth estimator used in this thesis is the Solve-the-Equation Plug-In (PI) approach. The PI approach is very similar to cross validation techniques. But it tends to oversmooth the UD a bit more. Generally the performance of the given bandwidth estimators is highly dependant on the presented data. For further details about each estimator Heidenreich et al. (2013) and the master thesis of (Zehnder, 2015) gives a good overview and backgrounds about other bandwidth estimators and their influence on the resulting UD.

A second parameter is the choice of the kernel. There are two types of kernels. Fixed ones for which the bandwidth stays the same for all data points and adaptive ones where the bandwidth is adaptive for different regions of the UD based on the locally measured densities. Adaptive kernels do smooth lower occurrences more than higher. So if we are interested in the full home range a fixed kernel is more appropriate and was applied in this thesis (Seaman and Powell, 1996). Overall the parametrisation does influence the results less then other factors like the given sample size and the temporal consistency (Powell and Mitchell, 2012b; Seaman and Powell, 1996). The KDE is a well established HRE with the advantage of a resulting UD instead of a binary boundary. The performance is highly dependent on the data, the bandwidth and the kernel selected and consequently high variations in estimation results occur. Other disadvantages are that KDE actually assumes statistical independence of the sample points which is not the case in this study and in many other movement ecology studies where autocorrelation between points is high (Section 4.1.3).

Parametrisation and method

For the estimation of KDE first the data was split in the before mentioned four research periods with the additional full data sets. Therefore we get 5 data sets. For all of them every individual was automatically filtered out. Then for every period the bandwidth of every individual was estimated with the ks package using four different methods REF,PI,BCV and SCV (Table 2.1). The broadly used least square cross-validation LSCV method for estimating the bandwidth could not be used because it fails when points are to close to each other (Wilson et al., 2020). Then a utilisation distribution for a given period and a given focal was calculated with help of the adehabitatHR package (Table 2.1). From the resulting UD the 50%, 95% and the 99% level was derived and saved. In the end we would have 600 home ranges for 10 individuals, 5 periods (4 partial periods + 1 full period), 4 different bandwidth approximator methods and 3 home range levels delineation (Core range, 95% HR and 99% HR). However, because not every individual was followed, the total number of derived home ranges was only 492.

4.1.7 Biased random bridges

Theory

The third main home range algorithm in this thesis is the Biased Random Bridge (BRB) estimator. The underlying concept is fundamentally different to the KDE approach. Instead of points the underlying trajectories between points, namely the Brownian bridges are used to estimate occurrence probability between two relocations. A Brownian random walk between two fixes is the underlying concept of Brownian bridges movement models. It describes a movement where any direction of the next step is independent of the one before. The utilisation distribution can be calculated by the formula 4.5. Generally the probability distribution looks like in 4.3. The density functions are mainly influenced by the time and distance between subsequent points. Additionally the location error is given as a parameter and assumed to be normally distributed over the point location. The main influential parameter is the Brownian motion parameter $\sigma_i^2(t)$. It describes the diffusion of an animal and is a proxy for how irregular the movement of an animal or species is (Horne et al., 2007; Zehnder, 2015). In the model, it is the highest between two relocations and 0 at the GPS-fixes. Therefore, we see a higher variance between points than at the fixes in figure 4.3. The biased random bridge is an adaption of this Brownian bridge movement model. It includes a drift part, which means that an animal does not move totally random between two relocations but has a directional bias. This means the resulting bridges or density functions are longer and lower between subsequent fixes if the drift coefficient is higher (Figure 4.3). More details about the BRB algorithm is given in Benhamou (2011).

$$df_{\mathrm{BB}}(z) = \frac{1}{T_{\mathrm{tot}}} \sum_{i=0}^{n-1} \left\{ \int_0^{T_i} \varphi(z; \mu_i(t), \sigma_i^2(t)) dt) \right\} \tag{4.5}$$

Variables and parts: $\varphi(z; \mu_i(t), \sigma_i^2(t))dt$ *= the bivariate density at any given time where* z *is any location,* μ_i *= mean which is proportional to time between fixes,* $\sigma_i^2(t)$ *= diffusion coefficient, variance term which is biggest between two fixes and 0 at fixes. It is estimated based on the movement trajectories of an individual,* T *= the duration of a bridge,* t *= the time evaluated between ranging between 0 and T. The formula of the Brownian bridge (Horne et al., 2007)*

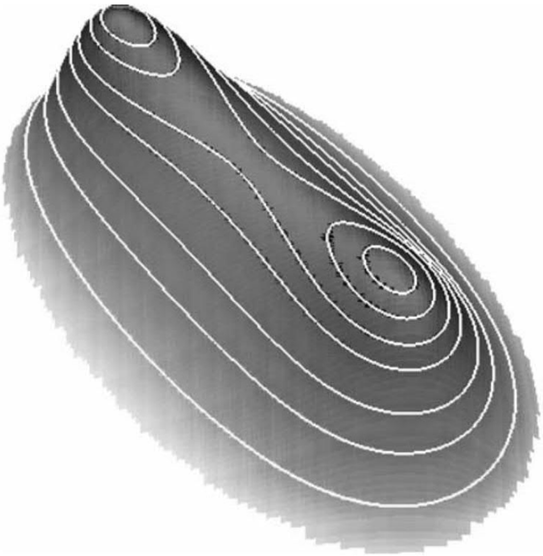


Figure 4.3 – Brownian bridge probability distribution. The density function estimates the probability at any given space between two relocations based on a biased random walk. Image from Horne et al. (2007).

Overall the BRB is a advanced third generation HRE which is mathematically not so easy to understand. It includes time, spatial positions as well as the trajectories for estimating home ranges. Which is different compared to KDE which only includes distances to other points and does not include the underlying trajectories at all. A main advantage is that BRB actually does explicitly need autocorrelated data (compared to KDE) because the algorithm uses the trajectories for estimating the utilisation distribution. It can also handle varying sampling intervals very well (Benhamou, 2011; Horne et al., 2007). On the other hand if autocorrelation or the sampling rate is too low the model based on random walk is becoming less useful although the BRB algorithm with its drift parameter can reduce this problem (Benhamou, 2011).

Parametrisation and method

Because of mathematical difficulties, the original algorithm of BRB has never been implemented in R instead the usage of a so called movement-based KDE has proved its worth. Differences of results to the original algorithm are negligible (Benhamou, 2011). For the estimation of BRB again the algorithm was applied to all four periods and the full research period using the adehabitatHR package. For all data, the default locational error of 12 m was used. The algorithm of BRB needs the parameter $\mathrm{h_{min}}$ (smoothing parameter describing the species related movement capacities, see above). As proposed by Benhamou and Cornalis (2010) the $\mathrm{h_{min}}$ can be estimated by summing the GPS-uncertainty with half the distance an individual is able to travel in a longer time period with its maximum empiric speed. Therefore a time period of 30 minutes, roughly the length of the sampling interval was chosen. The maximum velocity was retrieved for every individual-period combination with a cut off value of 99% to avoid outliers. After analysing the results it was decided to choose a global maximum speed value. The results of the preliminary analysis showed that maximum speed were in average 8.6±3.87 (ranging from 2.5 to 18) m per minute. A rather conservative value of 6 m per minute was chosen due to the slow behavioural movement pace and the relatively small areas they range in (**RQ A.1**). Additionally overall sinuosity indices show a relatively constant tortuosity which further speaks for a lower $\mathrm{h_{min}}$ value (Stark et al., 2017). The final $\mathrm{h_{min}}$ reference was calculated by multiplying the sampling interval of 30 min with the maximum empiric speed, dividing it by two and finally adding the relative positional uncertainty of 12 m. The resulting $\mathrm{h_{min}}$ was 102 m. Because the selection of $\mathrm{h_{min}}$ is based on the data set itself and is maybe sometimes a bit arbitrary an additional $\mathrm{h_{min}}$-factor was introduced. For every derived $\mathrm{h_{min}}$ reference eight possible weighting factors were multiplied (0.2,0.4,0.6, 0.8,0.9,1.1,1.2,1.4) to get the finally used $\mathrm{h_{min}}$.

Another parameter the $\mathrm{T_{max}}$ makes a temporal threshold. It defines the maximally allowed time between two GPS-Points to be added to the UD estimation. In our case, a value of 70 minutes to include bridges where one point was missing and an additional minimum threshold of 10 minutes was chosen if points were not sampled on a full half hour step.

The minimum movement threshold $\mathrm{I_{min}}$ which reflects the minimum amount of distance travelled to count as a movement, was chosen to be very low. Although Dürr and Ward (2014) proposed to use twice the distance of the locational uncertainty, a value of exactly

the locational uncertainty was used. Again, the reason was to not miss very short low scale movements, which are very typical for orangutans.
The last parameter which had to be defined was tau. It describes the duration of segments (steps) taken between two GPS-fixes where for every step a density function is fitted. A quick analysis of Zehnder (2015) showed negligible impact of the decision of choosing tau when calculating home ranges of far ranging lions (*Panthera leo*) and cheetahs (*Acinonyx jubatus*). A very conservative value, although it needs higher computational time, for tau with a duration of one minute was chosen. From the resulting UD the 50%, 95% and the 99% levels were derived and saved. In the end we would have 1200 home ranges for 10 individuals, 5 periods (4 partial periods + 1 full period), 8 different h_{min} (8 different weighting factors) and 3 home range level delineations (Core range, 95% HR and 99% HR). However, because not every individual was followed, the total number of derived home ranges was only 984.

4.1.8 Autocorrelated Kernel Density Estimation

Theory, parametrisation and method

A very new but mathematically very complex algorithm, the so called AKDE was also tested. Comparing to the KDE it overcomes the problem of violating the independence of sampling points problem. Highly autocorrelated data can therefore be analysed without violating statistical assumptions (Fleming et al., 2016). In this thesis the web interface proposed by Calabrese et al. (2021) was used. The web interface of ctmm allows to estimate home ranges via AKDE in a streamlined way. First the data for the 10 most followed females was uploaded and potential outliers were deleted. In our case only two points were additionally identified as outliers by their corresponding speed value. They were not already found in the preprocessing of the data set. Then a locational GPS-error of 12 m was set. Next the semi-variograms and peiodograms were visualised and explored. These diagrams reveal the underlying autocorrelation structure and the drift of a range. They show the average square distance travelled (y axis) for a given time lag (x axis). The semi variograms are the main tool for the AKDE to model movements based on the existing data. We can then select if we want to pool the variograms. This means that it tries to fit a population variogram instead of a variogram for each individual. This can be useful when movement behaviour between individuals is similar and we can reach a more robust semi variogram or the opposite if individuals like males and females are moving in a very different way. Then various continuous time movement models (Brownian Motion, Ornstein-Uhlenbeck motion, Integrated Ornstein-Uhlenbeck motion, Ornstein Uhlenbeck-F motion) are fitted to the empirical variograms. The best models are selected and home range UD are calculated by using the AKDE algorithm (Alavi, 2018; Calabrese et al., 2021; Fleming et al., 2016). The 50% delineation and 95% delineation of the utilisation distribution are downloaded locally and added to the other home range results.

4.1.9 Descriptors of home range

It is difficult to access which home range estimator or which parametrisation method works best for the orangutans of Suaq because we have no knowledge about the true home range distribution to validate and compare our results. What remains are descriptors of home ranges similar to a visual assessment.

Therefore, the resulting home ranges were analysed for their quality by using some descriptors (area, AUC, number of holes, number of polygons). The Area Under the Curve (AUC) was calculated which indicates if the relocations fit to the resulting home range isopleths (Walter et al., 2015). The AUC was calculated with the caTools package (1.18.2) (Tuszynski, 2021). AUC was already used for comparing HRE in a study of arboreal primate study by Stark et al. (2017). AUC values are ranging between 0.5 and 1, where 1 means a perfect agreement of GPS-points and the derived UD (Walter et al., 2015). The AUC reflects kind of a comparison of the HRE to a fine scaled grid cell method. The total area of the home ranges were calculated by the respective home range delineation. The number of polygons of which a home range consisted of was counted and the number of holes these polygons or the home range in total had was counted. Holes and polygons were only counted if they were bigger than 1000 m^2 to avoid small artefacts. This is approximately the area of twice the area of a circle with the locational error used of 12 m. Last but not least the compactness descriptor used in Zehnder (2015) was used which describes how compact a home range is. The idea is to reflect the efficiency of ecological use of space for their needs. The compactness was calculated as followed (Zehnder, 2015).

$$Compactness = \frac{4 * A}{\pi * D^2} \tag{4.6}$$

Variables: A = area of home range, D = diameter of smallest enclosing circle of all polygons.The formula to calculate compactness from Zehnder (2015).

4.1.10 Sensitivity to the number of locations

It is difficult to define the minimum number of observations which are needed to get reliable home range estimates. A simple way of estimating how many observations are needed to get a reliable home range for animals showing site fidelity is a bootstrapping approach where the home ranges are derived from an increasing percentage of data. Then the results can be visually analysed by plotting the home range size against the amount of data and the amount of data where the size of home ranges are approaching an asymptote can be used as a measure of the minimum locations needed (Laver and Kelly, 2010). To analyse the stability of home ranges and to determine the minimum number of points needed to get stable home ranges, this bootstrapping approach was implemented. An increasing amount of data was selected while applying the three main HRE (MCP, KDE, BRB). 5% of the data was used as a start and then an increment of 5% until 100% was added. For BRB the percentage of data was selected based on the percentage of follows instead of points, because the algorithm only calculates a UD based on a trajectory with reasonable temporal step-lengths (4.1.7). To be able to compare the results this approach was also chosen for MCP and KDE. This also makes sense for recommendations in field where an estimation of how many follows are needed to get a sense for a females home range makes more sense then the number of points. To analyse the effect of randomly subsampling the data set the above described bootstrapping process was also repeated 30 times but only for KDE as a compromise of calculation duration.

Because a shift in home range may occur, for example, due to socio-spatial dynamics between mother and daughter, the data was also subsampled temporally by calculating the home range after every month by the previous data gathered (Ashbury, 2013). For example the home range was calculated in August 2015 for the full data set until August 2015. Due to computational power this was again only done with the KDE algorithm.

4.2 Results

4.2.1 Sensitivity to sample size and home range sizes

The sample sizes were very different for each focal as already described in the overview of the data set (Section 2.2.1). For the three most tracked females, Ellie, Friska and Lisa, we can clearly see a stabilisation of the home range sizes for core ranges and the 95% HR. The core ranges approach an asymptotic behaviour at around 50 follows whereas for 95% HR the asymptotic behaviour is seen around 75 to 100 follows. For most other females apart from Tiara we see a start of stabilisation of the core range. However the 95% HR for Trident, Tiara and Sarabi are not really stabilising especially for MCP. The MCP algorithm generally reached an asymptote slightly earlier than the KDE and BRB. The MCP therefore stabilise earlier but a trend for stabilising is less visible when not a lot of data is available. Generally, all individuals with all algorithms showed an asymptotic behaviour compared to a linear one, which speaks for the usage of a stable ranging area.

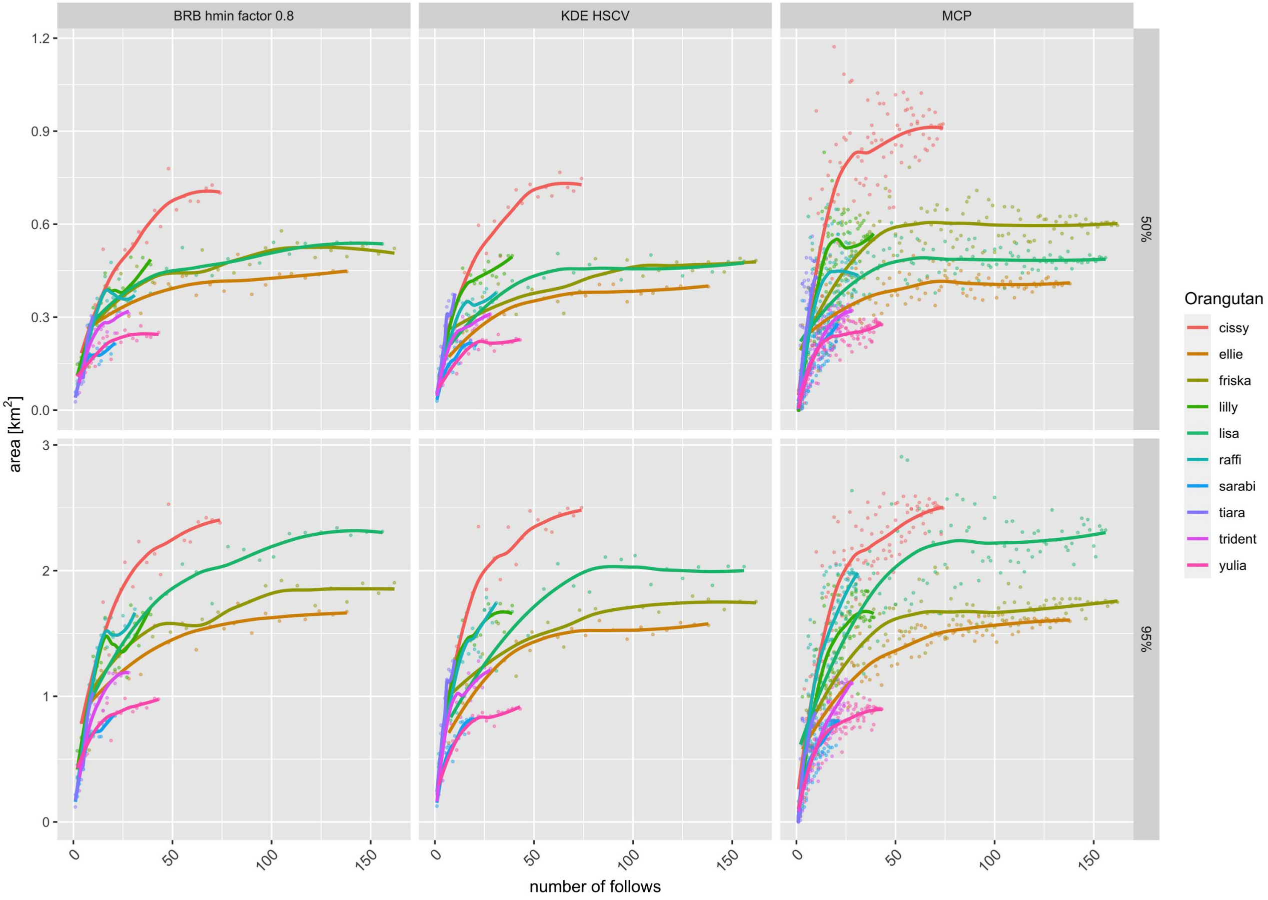


Figure 4.4 – Comparison of the stabilisation of home ranges.

4.2.2 Sensitivity to sample size

Random bootstrapped subsampling

The sensitivity of the random subsampling by the number of follows was also analysed by iterating over the subsampling process. The result for the KDE algorithm (with SCV bandwidth estimation) when repeating the subsampling for 20 times is shown in this graphic see Figure 4.5. Its clearly visible that core ranges do stabilise earlier than 95% HR. Already a relatively small sample size indicates the general home range size. Furthermore the ratio of core range to home range shows this ratio is relatively stable. The core range used by orangutans was around 27±6% (average of all periods and HRE) of the full home range (95%). Still there remains some difference between individuals. But when inspecting the changes over the year the ratio between core range and home range varies for most individuals between years and a LMM explaining the core range to home range ratio, with the research periods as a random effect, showed that only the individual Lisa had a statistically significant smaller core range to home range ratio over all periods (Lisa -0.06, p <0.05) (Figure C.2).

Temporal subsampling: Change of home ranges over time

The change of home ranges showed that many of the individuals had stable home ranges over the research periods and time. Especially core ranges were staying more stable than full home ranges. Trends for individuals are staying similar. Overall, many home ranges tend to change over the research period. Most of them increase and find a stable level but some even decrease quickly (Friska), which would indicate the clear stabilisation of a range or increase over the whole study period (Ellie). There are also quick increases and drops which either remained (Cissy) or disappeared (Raffi).

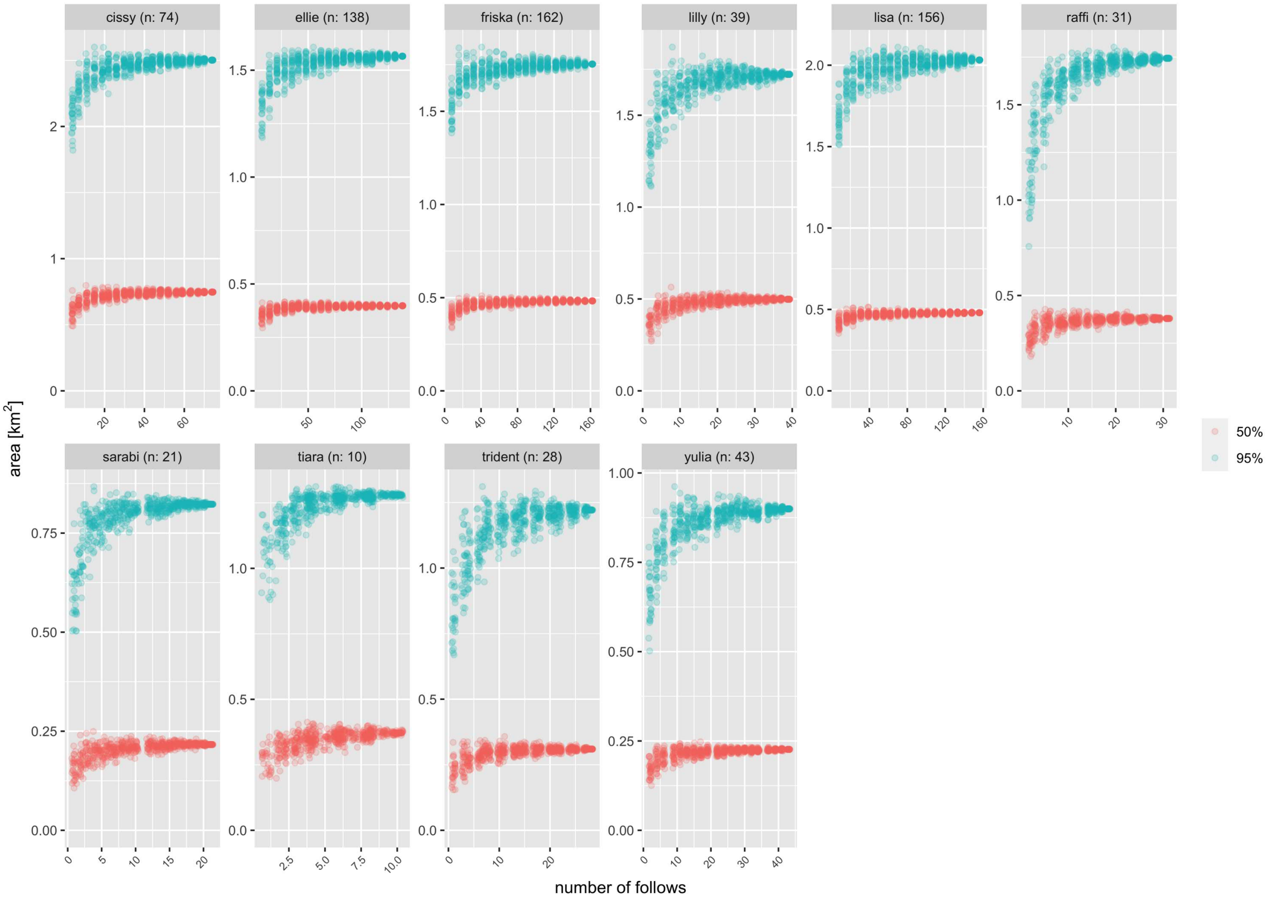


Figure 4.5 – Bootstrapped home range calculation for the KDE algorithm.

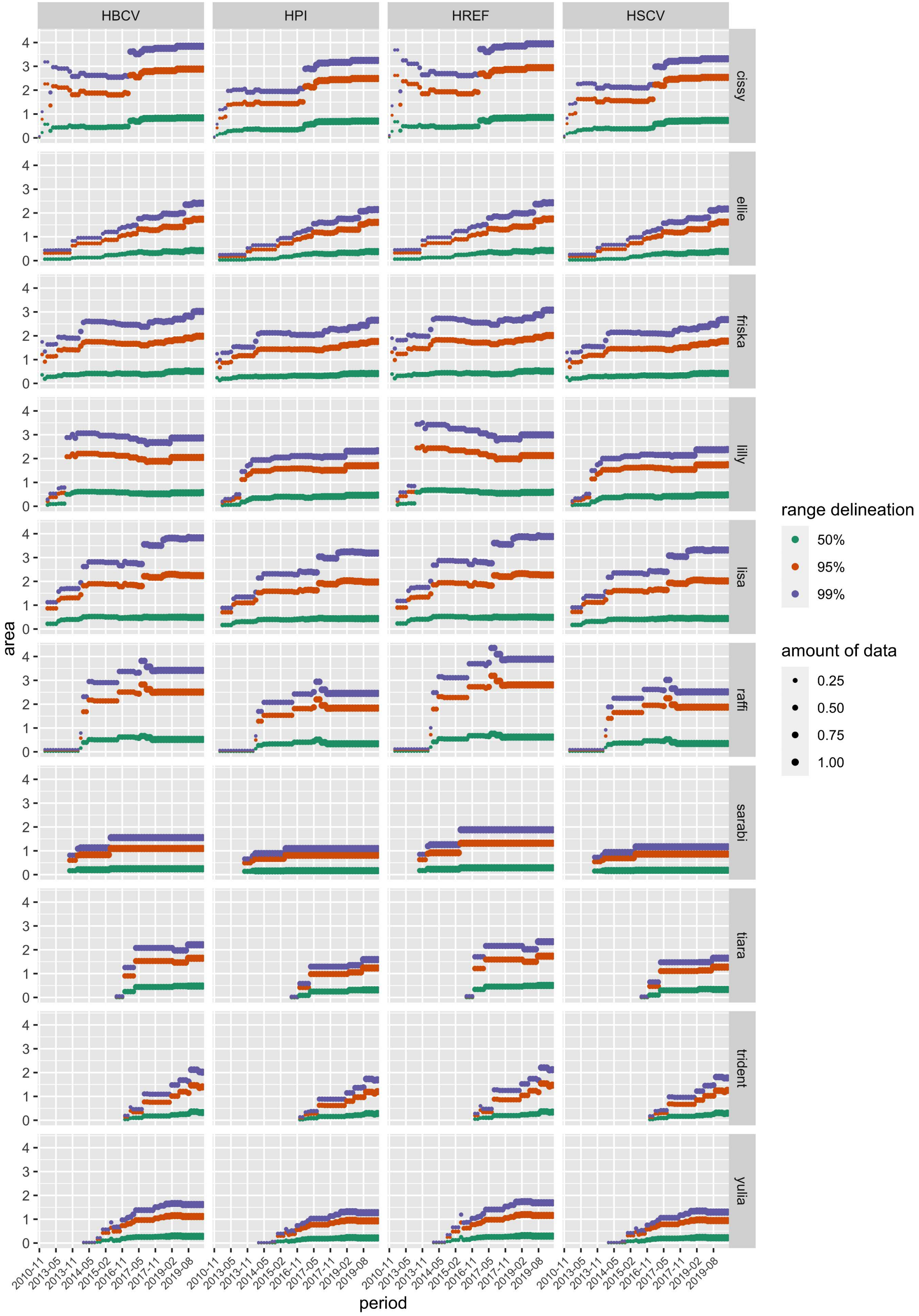


Figure 4.6 – The change of home ranges over time with different bandwidth estimator. For every date the cumulative amount of data was used to calculate the home ranges.

4.2.3 Evaluation of home range estimators

The following results were chosen to reduce the amount of data. For every HRE the parametrisation was analysed and reduced. For KDE the bandwidth estimator was chosen. For BRB the scaling of the smoothing parameter was chosen. Whenever comparing parametrisation, or different algorithms the values for the home range descriptors were scaled between 0 and 1. This makes it easier to visually compare the results. For parametrisation comparison of HRE the values were divided by the maximum of the observed values per group. For example the bandwidth approximators (BCV,SCV,PI,REF) for KDE per individual and periods were compared while dividing by the maximum of the period-individual groups. When looking at Figure 4.7 its probably clear whats meant by normalisation per group.

Parametrisation of KDE

For the calculation of home ranges via the KDE algorithm the bandwidth was estimated with four methods. First looking at general patterns its pretty obvious that two groups of bandwidth estimators are very similar (Figure 4.7 and Table C.2). On the one hand the BCV and the reference method showed very similar values for estimated home range area and compactness. Just for Raffi and Sarabi the values between BCV and the reference method differed slightly around 10 to 20%. On the other hand were PI and SCV almost identical for all individuals and home range delineations. The difference between these two groups (BCV/REF, PI/SCV) for the estimated home range sizes were about 10 to 40%. Higher discrepancies between the bandwidth methods mostly occured with orangutans which were tracked less frequently like Tiara, Raffi and Sarabi. Differences between the two groups especially for compactness and number of polygons were more apparent for core ranges and for ranges with the delineation on the level of 99%. The ranges split more when more extreme values are included or when highly used regions are delineated. Holes in the home ranges were relatively rare especially for core ranges where only Ellie showed signs of holes in the core range when using the two algorithms PI and SCV with less smoothing. In figure 4.6 we see the reaction of the HR size on the bandwidth estimation method when slowly adding data over time. Again the BCV/REF method behaved differently than the PI/SCV method. The BCV/REF varied much more when sample size was small. These two methods generally estimated a much bigger home range based on very few points. Whereas the other two methods PI/SCV showed a slow increase of the home range in the beginning. Which is a more intuitive behaviour because the minimum amount of data to estimate a home range reliably is similarly derived by the asymptotic behaviour of a bootstrapped subsampling process (Section 4.2.1). In the case of Cissy and Friska we can argue that the BCV/REF gives a better HR estimation in the beginning when very few data is sampled. Nonetheless, most importantly, the amount of data is most crucial when approximating a home range reliably. For most individuals, the home range and especially the core range stayed relatively stable over time. The 95% and the 99% home ranges showed more variation, for example, with an overall increase of the 95% home range size by the intensely followed Lisa around the year 2017, when the core range on the other side, stayed relatively stable. To know if this increase is of behavioural nature (e.g., shift of home range or excursions based on ecological or social pressures) or is based on missing data in the previous years is difficult. When looking at the home range changes of Ellie, another intensely sampled individual, the changes showed an ever increasing size of the outer home range boundaries where again the core range stayed relatively stable. Overall, the bandwidth estimator PI generated the most complex not compact home ranges closely followed by the SCV. The reference method on the other hand smoothed home ranges the most and had the least polygon counts or holes with a high compactness index. Nonetheless when analysing the results visually all the used bandwidth estimators resulted in valid home ranges. The values of AUC show a better overall fit and performance of the group of PI and SCV. The values are the same for core range and both other home range delineations because the AUC value is derived from the UD. But AUC was high for all of the used bandwidth estimator. Following these results the home ranges estimated with the SCV bandwidth estimator was used for further analysis if the amount of data had to be reduced. This selection may underestimate or under smooth home ranges but definitely does not show oversmoothing over the research area.

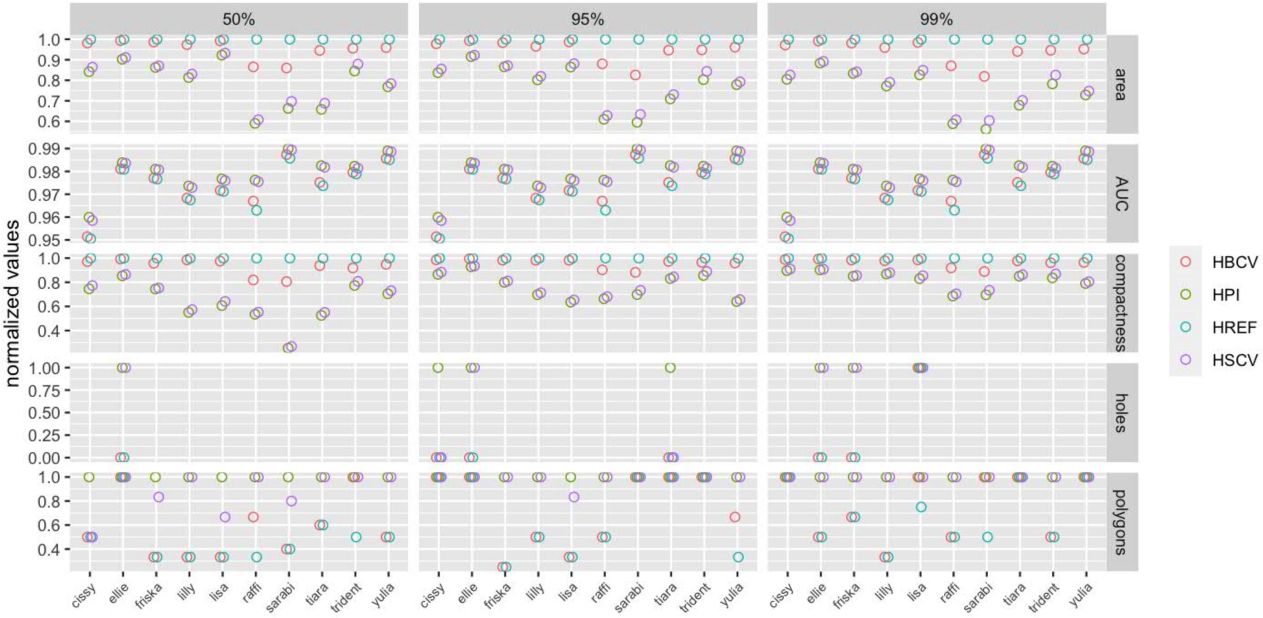


Figure 4.7 – Home range descriptors with varying bandwidth estimators.

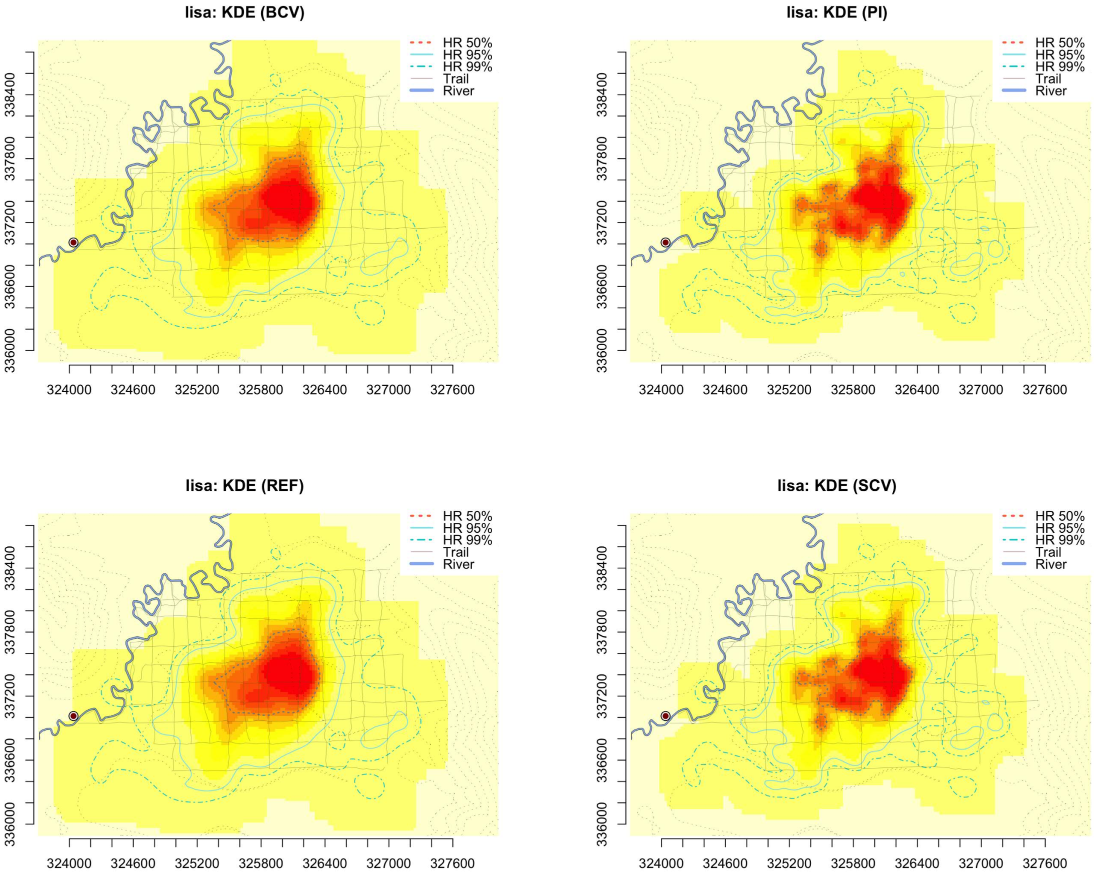


Figure 4.8 – Home range of Lisa estimated with different bandwidths and the KDE algorithm for the total research duration.

Parametrisation of BRB

For accessing the influence of the smoothing parameter $\mathrm{h}_{\mathrm{min}}$, the HRE descriptors number of holes, area, number of polygons and the compactness values were used. Generally the variation of $\mathrm{h}_{\mathrm{min}}$ showed a relatively linear relationship to slightly exponential relationship. For polygon counts, compactness and AUC the decrease was steeper than a linear decrease (Figure 4.9). Because a simple scaling factor was introduced, changes in the descriptors are following this scaling either up or down. This is different from the analysed difference in bandwidth estimators before because the scaling factor is interdependent. But it allows us to see when strong differences happening or when first holes in the core region or full home ranges occur. Looking at the home range areas the decrease in size was around 50% when using only a fifth of the derived $\mathrm{h}_{\mathrm{min}}$. Increase or decrease in area based on the scaling factor was the same for core ranges as for the full ranges. Compactness differed much more for core ranges when varying h_{min}. The number of holes were mainly rising when using scaling factors below 0.6. The number of holes were much higher for the full home ranges than for core ranges but even for core ranges they appeared for some individuals. Similarly the number of polygons were lowest for a high scaling factor and started to drop significantly when having a scaling factor below 0.8. The AUC increased clearly when using a smaller h_{min}. Finally for further usage the h_{min} factor of 0.9 was chosen. It is chosen very near to the initial approximation of h_{min} but slightly lower to reach slightly higher AUC but without getting too many holes and polygon counts (see example 4.10). The HR were also inspected manually to check if they had a reasonable shape and were not extremely under- or oversmoothed. Generally again we used a value which leads to slightly more under smoothing which was also the case for the chosen bandwidth estimator for the KDE algorithm.

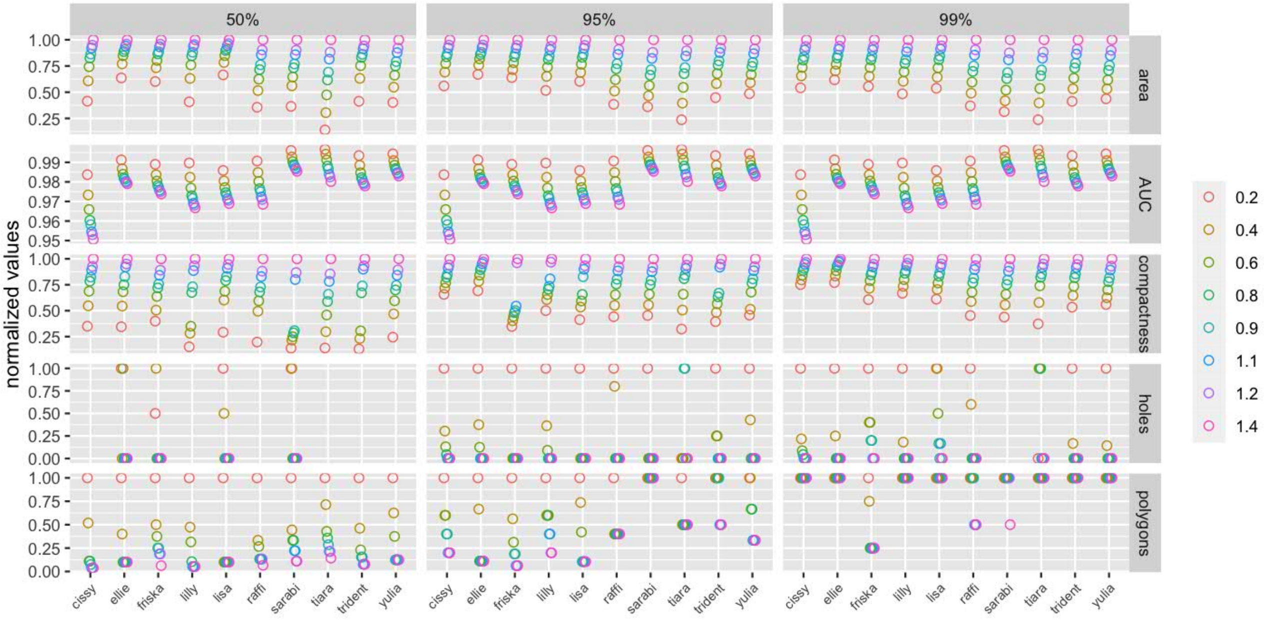


Figure 4.9 – Home range descriptors with varying h_{min}.

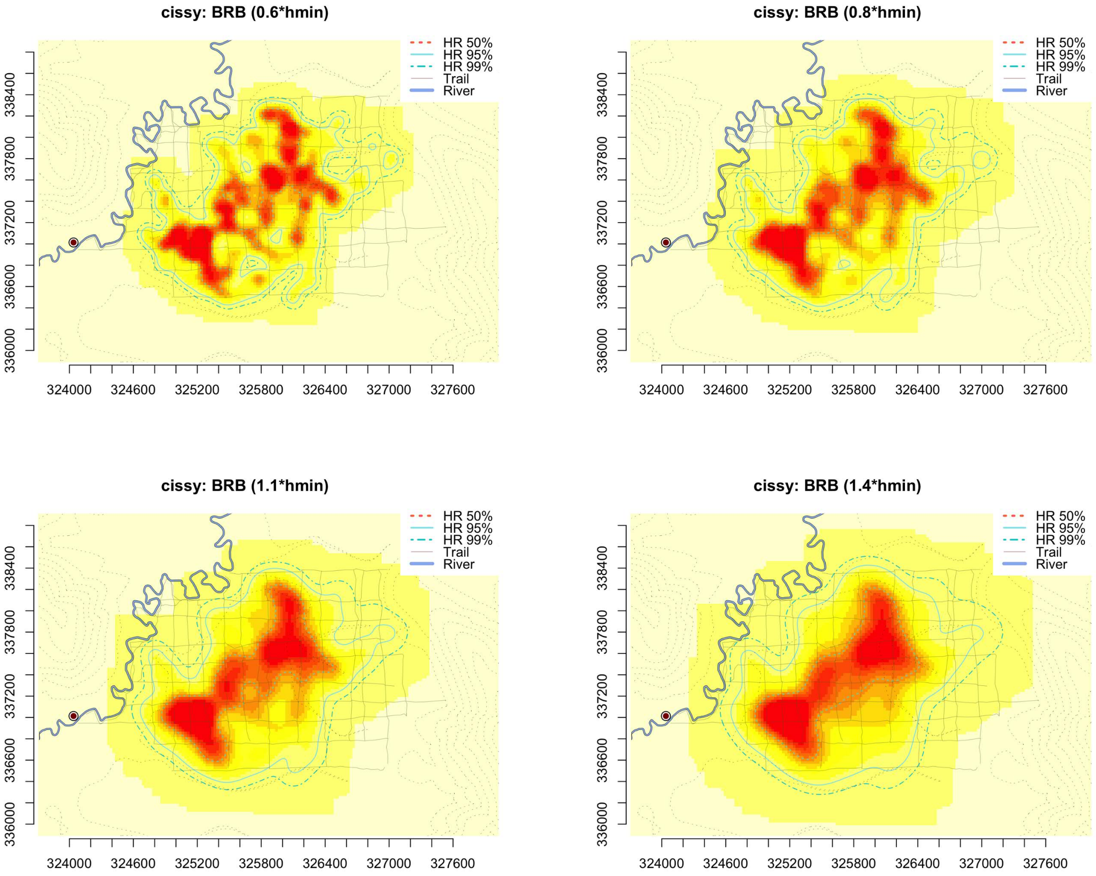


Figure 4.10 – Home range of Lisa estimated with BRB algorithm for the total research duration.

Home range estimator comparison

For the following comparison, core ranges, 95% home ranges and 99% home ranges were used if available. The four algorithms used were compared by again looking at the HR descriptors. For AKDE the HR results were used which did not originate from a pooled variogram fit. But a quick analysis did not show any difference for the pooled or unpooled approach when looking at the derived movement parameter. The variograms of the most often tracked females also revealed an approaching asymptote after a time lag of around 15 to 30 days. This means an individual normally fully crossed its home range after 15 to maximally 30 days (Calabrese et al., 2016). For KDE only the results estimated with the SCV bandwidth estimator were used and for BRB the results with a h_{min} of 0.8 were used. MCP did not need any parametrisation and therefore we used all the results.

The AKDE approach using the ctmm shiny web application produced the biggest home ranges compared to all other HRE and for all individuals. For home ranges with large sample numbers (Friska, Ellie, Cissy, Lisa) the differences were smaller. Additionally differences of the core ranges from the other HRE's to the AKDE home ranges were smaller for core regions and highly sampled individuals. The difference between AKDE and the other estimators were on average around 26% in average for core regions, 36% for the 95% delineation and 43% for the 99% delineation. The difference if the absolute area was tested with a Kruskal-Wallis test and showed a clear difference between AKDE and the other home range estimators (Kruskal-Wallis, df = 3, $\tilde{\chi}^2 = 9.378$, p = 0.024). Differences for MCP, KDE and BRB were lower and statistically not significant for all delineations (Kruskal-Wallis, df = 2, $\tilde{\chi}^2{}_{50\%} = 0.71$,$\tilde{\chi}^2{}_{95\%} = 0.034$, $\tilde{\chi}^2{}_{99\%} = 0.7$, $p_{\text{all}} > 0.1$). When only comparing these three HRE we find the biggest values for the core ranges with the MCP approach (Figure C.1). Differences between the MCP core ranges and the core ranges of KDE and BRB were ranging from 10 to 30%. Differences were smaller for the 95% and 99% home ranges and the trends for one of the algorithms were not so clear. For the 99% home ranges every of the three algorithms even once reached the highest value.

The AUC showed no strong differences between the two algorithms BRB and KDE. However compactness did show clearly higher values for results calculated with the MCP approach especially in the core ranges. After MCP the AKDE approach reached second highest values for compactness especially for the full home ranges whereas BRB and KDE showed similarly low values over all delineations. Therefore it does not surprise that the BRB and KDE had the most holes in the ranges and the highest number of polygons. Especially KDE showed more polygons in the core region and the highest delineation 99% than the other HRE. Holes did occur more often in core ranges than the other home range delineations.

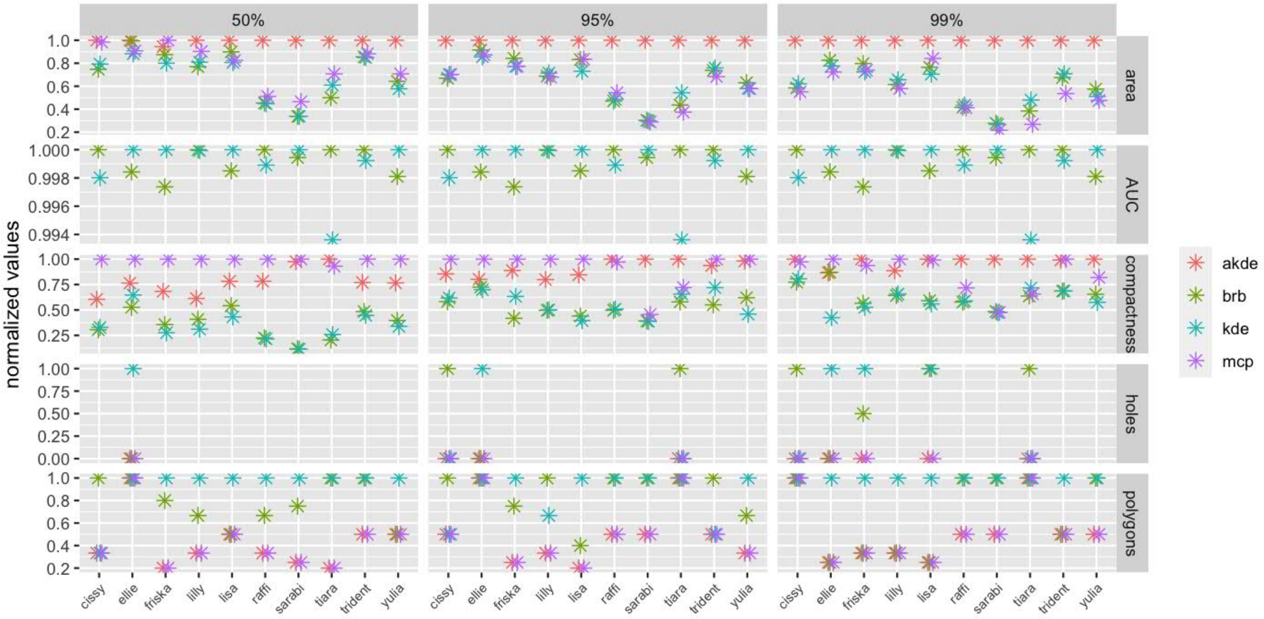


Figure 4.11 – Home range descriptors of all HRE used. The values are normalised per highest value of the category for better comparison.

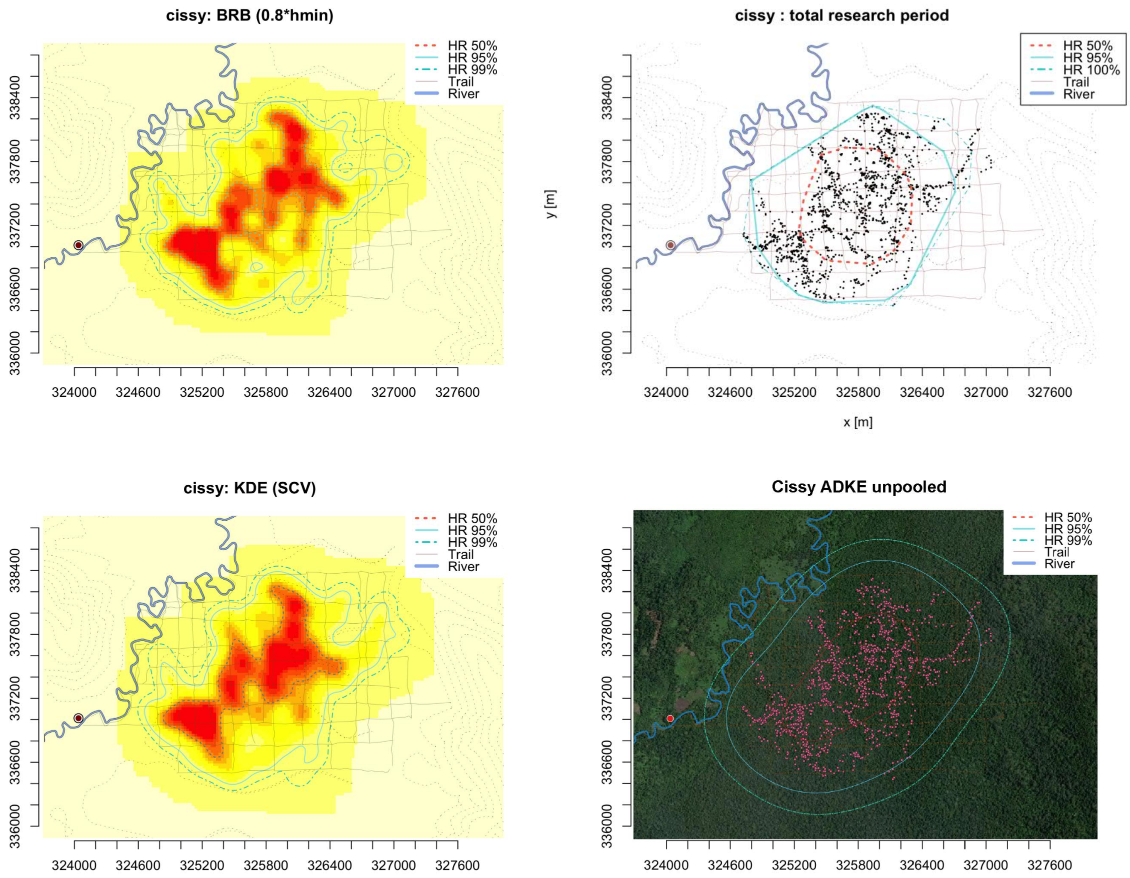


Figure 4.12 – Comparison of home ranges calculated with different algorithms. Here the home range for the total research period for Cissy. Derived by the MCP, KDE, BRB and AKDE method.

4.2.4 Home ranges

The resulting home ranges over all research periods and the total research period for the 10 most tracked females were ranging between 0.8 (algorithm: MCP, focal: Sarabi) and 3.59 km^2 (algorithm: AKDE, focal: Raffi) with a mean of 1.78±0.7 km^2. The core ranges ranged between 0.21 (algorithm: BRB, focal: Sarabi) and 0.93 km^2 (algorithm: AKDE, focal: Cissy) with a mean of 0.45±0.18 km^2. Variation between individuals is therefore just slightly bigger for the full home ranges than for the core ranges. The home ranges derived from the total research period were mostly bigger than for only one of the periods (see box plots and dots in figure 4.13). Generally, the home range sizes were bigger for individuals with a larger sample size. For Cissy and Lilly, the core range increased by up to 100% when using the total research period, likewise did the full home range. This indicates that the research periods we used arguably did not have enough data as described in Section 4.2.1. Still, a high variation of home range sizes is visible and individual differences exist. The core ranges were mostly proportional to the full home ranges.

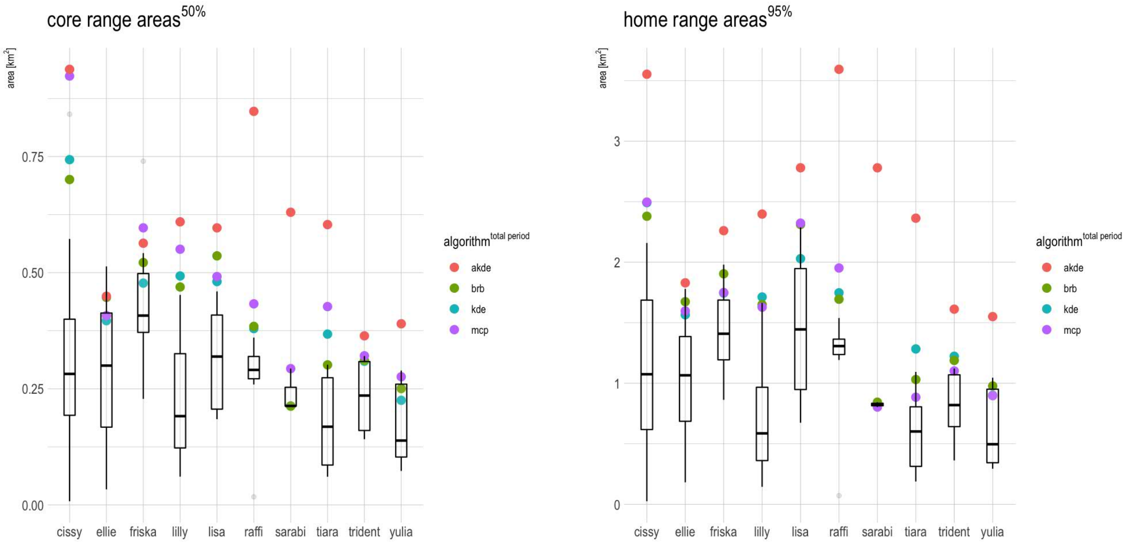


Figure 4.13 – Home range sizes per individual for core ranges and full home ranges. The box plots represent home ranges derived for all of the four research periods itself.

4.2.5 Explaining home range sizes

A LMM explaining the ranging area was fitted to analyse the influence of fruit trees in the home range, the dominance category of the female, the mean DJL over all years and age categories. Additionally, the number of follows was included as a fixed effect explaining the home range sizes. Only the home ranges from the total research period were used because we were mainly interested in the absolute range values when having a stable home range. Furthermore, the data set is, as discussed before, very unbalanced, especially for some research periods. Due to high co-linearity between age categories and dominance groups only the dominance categories were kept (Kruskal-Wallis, df = 3,$\tilde{\chi}^2$ = 7.26, p = 0.064).

Core ranges

The LMM for the null model with only the individual as a random effect explained around 60 %. The null model with only the type of algorithm as a random effect (MCP, KDE, BRB, AKDE), explained around 12 %. For the model, both the algorithm and the individual were

Table 4.2 – Statistical models trying to explain the home range size for the full study duration.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	Core range size	Intercept	intercept	-0.1681	-0.9857 – 0.6495	0.687	-
	n = 32	Dominance	Predictor	-0.0789	-0.1850 – 0.0271	0.145	1.697897
	P = 0.00745**	Normalized fruit trees	Predictor	5.1413	0.9796 – 9.3031	**0.015**	1.207517
	M-R2 = 0.414	Num. follows	Predictor	0.0008	-0.0001 – 0.0018	0.077	1.226905
	C-R2 = 0.902	Avg. DJL	Predictor	0.0003	-0.0007 – 0.0013	0.568	1.666834
	Family = Gaussian	Focal	Random	-	-	0.17	-
		Algorithm	Random	-	-	0.21	-
b)	Home range size	Intercept	intercept	-1.0386	-4.8657 – 2.7886	0.595	-
	n = 36	Dominance	Predictor	-0.2719	-0.6265 – 0.0827	0.133	1.99135
	P = 0.0125*	Normalized fruit trees	Predictor	26.3397	-0.0314 – 52.7108	0.05	1.115309
	M-R2 = 0.311	Num. follows	Predictor	0.0033	0.0000 – 0.0066	**0.049**	1.181032
	C-R2 = 0.885	Avg. DJL	Predictor	0.0007	-0.0025 – 0.0039	0.69	1.907411
	Family = Gaussian	Focal	Random	-	-	**0.0004**	-
		Algorithm	Random	-	-	**0.0003**	-

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; ***** model better than the null model; Statistical variables info's see first table

used as random effects. The full model was better (p<0.001) than the null model (Δ AIC in Table 4.2). The full model explained around 90 % of variation where the fixed effects explained around 41 % of the variation.

Home ranges

The null model with only the focal as an explanatory variable again did explain most of the variation in the home range size (conditional $R^2 = 0.45$). The algorithm as a random effect explained around 28 % of variation, slightly more than for the core ranges which reflects the slightly higher variation in home range sizes for different algorithms (section 4.2.4). The full model was again better than the null model (Δ AIC in Table 4.2, p = 0.0104). The full models fixed effects and random effects together explained around 88 % of variance (conditional $R^2 = 0.882$) in area, whereas the fixed effects alone explained around 31 % of variation in area.

Explanatory variables

The matrilines, which are not included in the LMM because the amount of data would have been reduced, did differ slightly for core ranges and even more for the full home ranges but this difference probably originates from the difference in sampling effort per matriline (Figure C.3). When comparing different years and comparing the home range sizes for the matrilines researched, it becomes clear that the variation largely results from the amount of data gathered per matriline.

The number of follows as a measure of sampling rate did explain some of the variation of the size of core ranges and full home ranges even when corrected for every individual's sampling rate and the algorithm used for the HR calculation. For the full home ranges the number of follows explained an additional 7 m^2 per additional follow and for core ranges the increase corresponded to only 7 m^2 per follow. The DJL as a movement parameter was not explaining the size of home ranges but was positively related to the size of HR (Table 4.2).

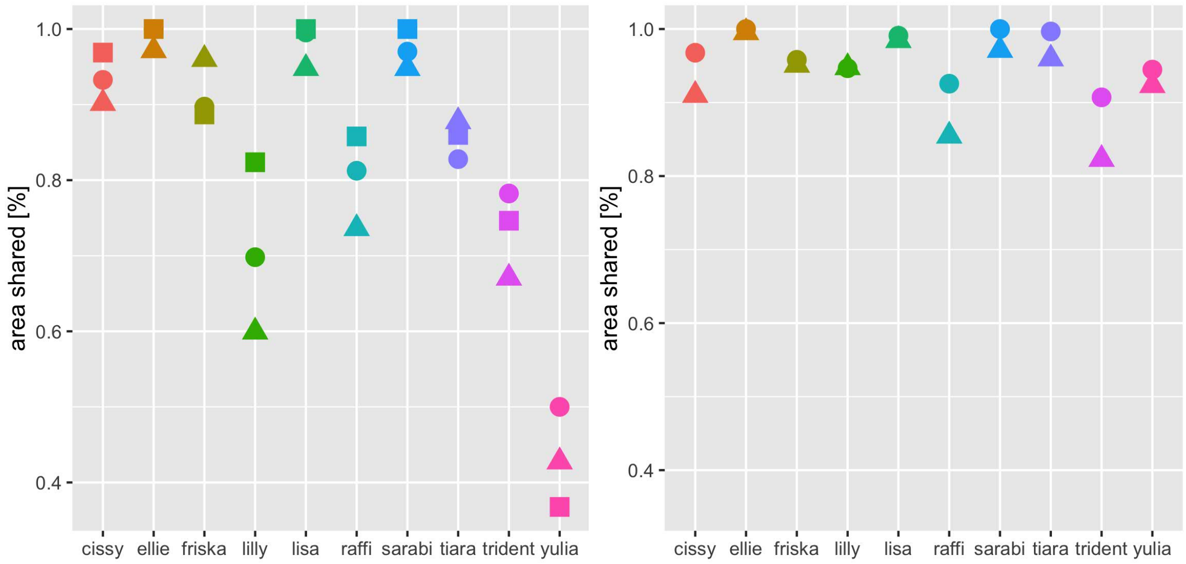
The full model showed a statistically not significant effect of dominance and its colinear variable age category. Nonetheless, core ranges were in average 77 m^2 bigger for every stronger dominance category. The full home range increased by 270 m^2 for every higher dominance category (similar for age).

The fruit trees did show a positive effect on core range size when correcting for individuals and the algorithm used, which was statistically more pronounced in the core ranges than the full home ranges. For a decrease in 1% of normalised fruit trees (normalised fruit trees = percentage of fruit trees to the full sample effort), the core range area increased by 50 m^2. The full home ranges even increased by 260 m^2 per 1% increase in normalised fruit trees.

4.2.6 Home range overlaps

Total area shared per individual

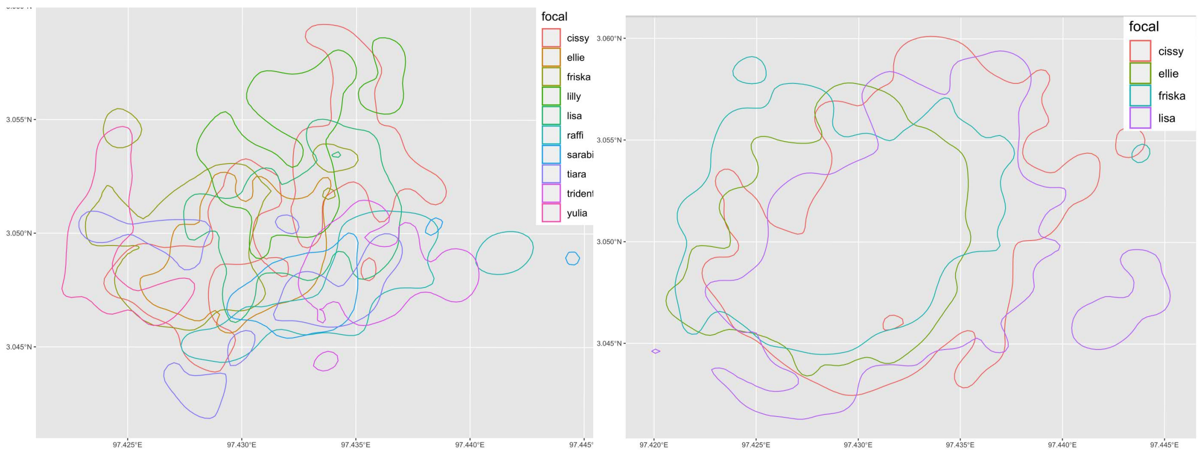
Home range overlaps were derived by various types of indicators. Overlaps were calculated for all research periods but also for the total research period. For the analysis, only the overlaps for the total research period were included for the same reasons as for the home range analysis (Section 4.2.4). The individuals were included as random effects as well as the period and the algorithm. The full home ranges were shared to a higher percentage than the core areas (Figure 4.14). Looking at the four females which were sampled the most showed that the area shared was almost 100% for core ranges. For the full home ranges the values were slightly higher than for core ranges (Figure 4.15). In average, the relative overlap for core ranges was 84% and for home ranges it was 96%. The home ranges of the individuals, which were less frequently followed, showed clearly lower values for core ranges than for the full home ranges. Looking at the map of all core ranges suggests that overlaps are even for core ranges very high and that lower overlaps are especially dependant on the centrality to the research area.



(a) core range

(b) home range

Figure 4.14 – Percentage of shared ranging area by individual for core ranges **(a)** and 95% HR **(b)**. The values are derived from the home range areas derived by the MCP (■), BRB (◯) and KDE (△).



(a) all core ranges (BRB)

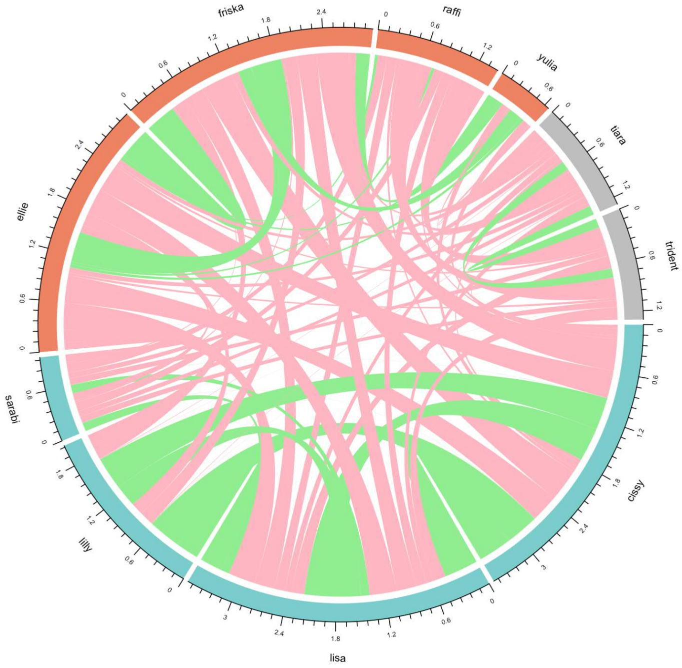
(b) selected home range

Figure 4.15 – Home ranges **(a)** and core ranges **(b)** of the four most tracked individuals.

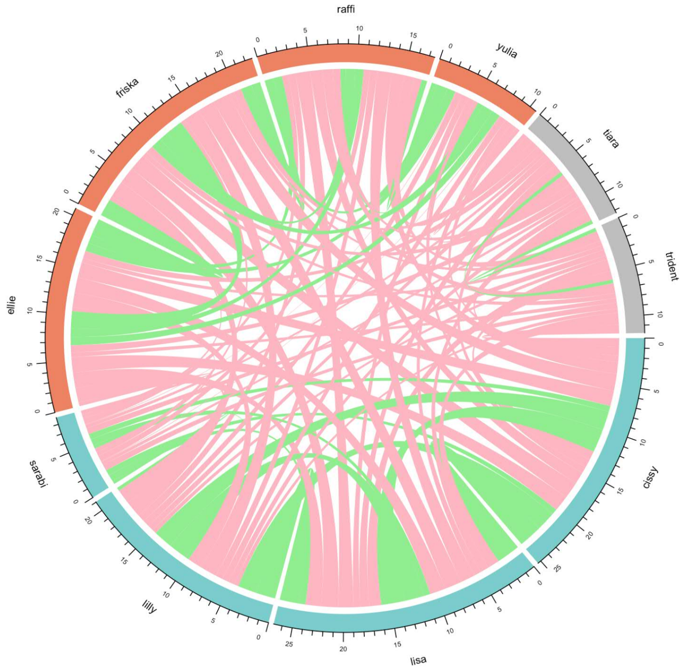
Overlaps and overlap indices

The overlap indices, namely the Jaccard Index, the BA, the UDOI and the Volume of Intersection highly correlated with each other with a correlation coefficient around 0.95 and higher (Pearsons's correlation coefficient Table C.5). The overlap areas likewise did show high correlation with the overlap indices. The overlap sizes relative to the home range sizes showed a slightly lower correlation with the other overlap indices. For further comparison the

UDOI which according to Fieberg and Kochanny (2005) gives the most expressive results, the Jaccard overlap, the overlap area and the relative overlap were used. The visual inspection showed that core ranges had bigger proportional overlaps and some home ranges did have much less overlapping areas as others (Figure C.7). The Jaccard overlap and the relative overlap did show a statistically clear positive impact of relatedness of females for the full home ranges but not for core ranges.



(a) absolute core range overlaps



(b) absolute home range$^{95\%}$ overlaps

Figure 4.16 – Overview of overlaps between individuals over total research period. Overlaps were derived from the BRB algorithm with a h_{min} scaling factor of 0.8. Overlaps shared with related individuals are indicated with green and overlaps shared with unrelated individuals are marked in red. The matrilines are marked in orange, blue and grey. The absolute overlap values show the cumulative sum of overlapping areas [km^2] per individual. The UDOI and the relative HR shared were calculated from the UD and not from the polygons and are shown in the appendix (Figure 4.16).

4.2.7 Explaining overlap indices

For the absolute overlap values, the relation of females had a positive effect. For core ranges the LMM predicted an increase of absolute overlaps by only 21 m^2 and for home ranges it predicted an increase of 160 m^2. The difference in dominance showed not to significantly explain the overlapping area (see also Figure C.6). The estimated slope and therefore the increase of overlap when individuals had a higher dominance difference were minimal (CR: 11 m^2,HR: 30 m^2).

Relatedness significantly positively impacted the Jaccard index and relative overlaps of full home range overlaps but was not significant in explaining core range Jaccard index and relative overlaps. Dominance difference significantly positively impacted the Jaccard index and relative overlaps of full home ranges as well as core range relative overlaps, but was not significant in explaining core range Jaccard index.

The last overlap indices which is arguably the most expressive estimator because it uses the underlying UD instead of a polygon delineation of overlap was the the UDOI. The difference in dominance showed a statistically not significant effect of only 42 m^2 per difference in dominance category (4 categories). The UDOI increased clearly when individuals were related by around 10 %. All overlap indices for the full home range increased within matrilines compared to non related individuals when comparing the values directly without a LMM. The core ranges were also overlapping more when individuals were related, but the change was less strong (Figure C.4).

4.2.8 Fruit trees in home ranges and overlaps

In the core ranges (BRB, h_{min} factor 0.8) of Cissy, Ellie, Friska, Lilly, Trident and Lisa, the normalised fruit tree value showed to be slightly higher than in the full home ranges (Figure C.2). For the other individuals, the opposite was the case. In average, core ranges, home ranges and overlaps did not differ in the value of normalised fruit trees (Figure 4.17). A LMM with the algorithm and the individual as random effects, which was fitted to explain the number of fruit trees in the overlaps, did not find any difference between related and unrelated individuals. Moreover, the dominance difference or the age category difference did not indicate any influence of these two variables on the normalised fruit tree value of

Table 4.3 – Statistical models trying to explain the overlap indices. For the absolute overlaps, the Jaccard Index and the relative overlap all research periods were included and a random effect was introduced for each research period.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P
a)	Absolute overlap (CR)	(Intercept)	intercept	0.07	0.02 – 0.12	**0.005**
	n = 480	Dominance diff.	Predictor	0.01	-0.00 – 0.02	0.089
	P = 0.016*	Related	Predictor	0.02	0.00 – 0.04	**0.03**
	M-R2 = 0.016	Focal	Random	-	-	**<0.0001**
	C-R2 = 0.197	Period	Random	-	-	**<0.0001**
	Family = Gaussian	Algorithm	Random	-	-	**<0.001**
b)	Absolute overlap (HR)	(Intercept)	intercept	0.42	0.12 – 0.71	**0.005**
	n = 678	Dominance diff.	Predictor	0.03	-0.01 – 0.07	0.121
	P <0.0001***	Related	Predictor	0.16	0.10 – 0.22	**<0.001**
	M-R2 = 0.027	Focal	Random	-	-	**<0.0001**
	C-R2 = 0.448	Period	Random	-	-	**<0.0001**
	Family = Gaussian	Algorithm	Random	-	-	**<0.0001**
c)	Jaccard (CR)	(Intercept)	intercept	0.13	0.08 – 0.18	**<0.001**
	n = 480	Dominance diff.	Predictor	0.01	-0.00 – 0.03	0.145
	P = 0.115	Related	Predictor	0.02	-0.01 – 0.05	0.168
	M-R2 = 0.009	Focal	Random	-	-	**<0.0001**
	C-R2 = 0.068	Period	Random	-	-	**<0.0001**
	Family = Gaussian	Algorithm	Random	-	-	**<0.0001**
d)	Jaccard (HR)	(Intercept)	intercept	0.18	0.10 – 0.26	**<0.001**
	n = 678	Dominance diff.	Predictor	0.02	0.00 – 0.03	**0.016**
	P <0.0001***	Related	Predictor	0.08	0.06 – 0.10	**<0.001**
	M-R2 = 0.056	Focal	Random	-	-	**0.002**
	C-R2 = 0.318	Period	Random	-	-	**<0.0001**
	Family = Gaussian	Algorithm	Random	-	-	**<0.0001**
e)	Relative overlap (CR)	(Intercept)	intercept	0.23	0.16 – 0.30	**<0.001**
	n = 480	Dominance diff.	Predictor	0.03	0.00 – 0.06	**0.025**
	P = 0.115	Related	Predictor	0.02	-0.02 – 0.07	0.276
	M-R2 = 0.015	Focal	Random	-	-	**0.045**
	C-R2 = 0.075	Period	Random	-	-	0.999
	Family = Gaussian	Algorithm	Random	-	-	**0.0005**
f)	Relative overlap (HR)	(Intercept)	intercept	0.36	0.28 – 0.43	**<0.001**
	n = 678	Dominance diff.	Predictor	0.03	0.00 – 0.05	**0.028**
	P <0.0001***	Related	Predictor	0.11	0.07 – 0.15	**<0.001**
	M-R2 = 0.047	Focal	Random	-	-	**0.003**
	C-R2 = 0.12	Period	Random	-	-	**0.0002**
	Family = Gaussian	Algorithm	Random	-	-	**0.019**
g)	UDOI (UD)	(Intercept)	intercept	0.24	0.12 – 0.36	**<0.001**
	n = 678	Dominance diff.	Predictor	0.05	-0.01 – 0.10	0.082
	P = 0.021*	Related	Predictor	0.09	0.00 – 0.18	**0.045**
	M-R2 = 0.047 / C-R2 = 0.2	Focal	Random	-	-	**0.17**
	Family = Gaussian	Algorithm	Random	-	-	**0.002**

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; $^{\cdot}p < 0.1$; CR = Core range$^{50\%}$; HR = home range$^{95\%}$; UD = utilization distribution$^{95\%}$; bold = significance level reached; Statistical variables info's see first table overlaps in the full home ranges. For core ranges interestingly the normalised fruit tree value increased with difference of dominance between individuals similarly to the overlap indices above (Table C.7).

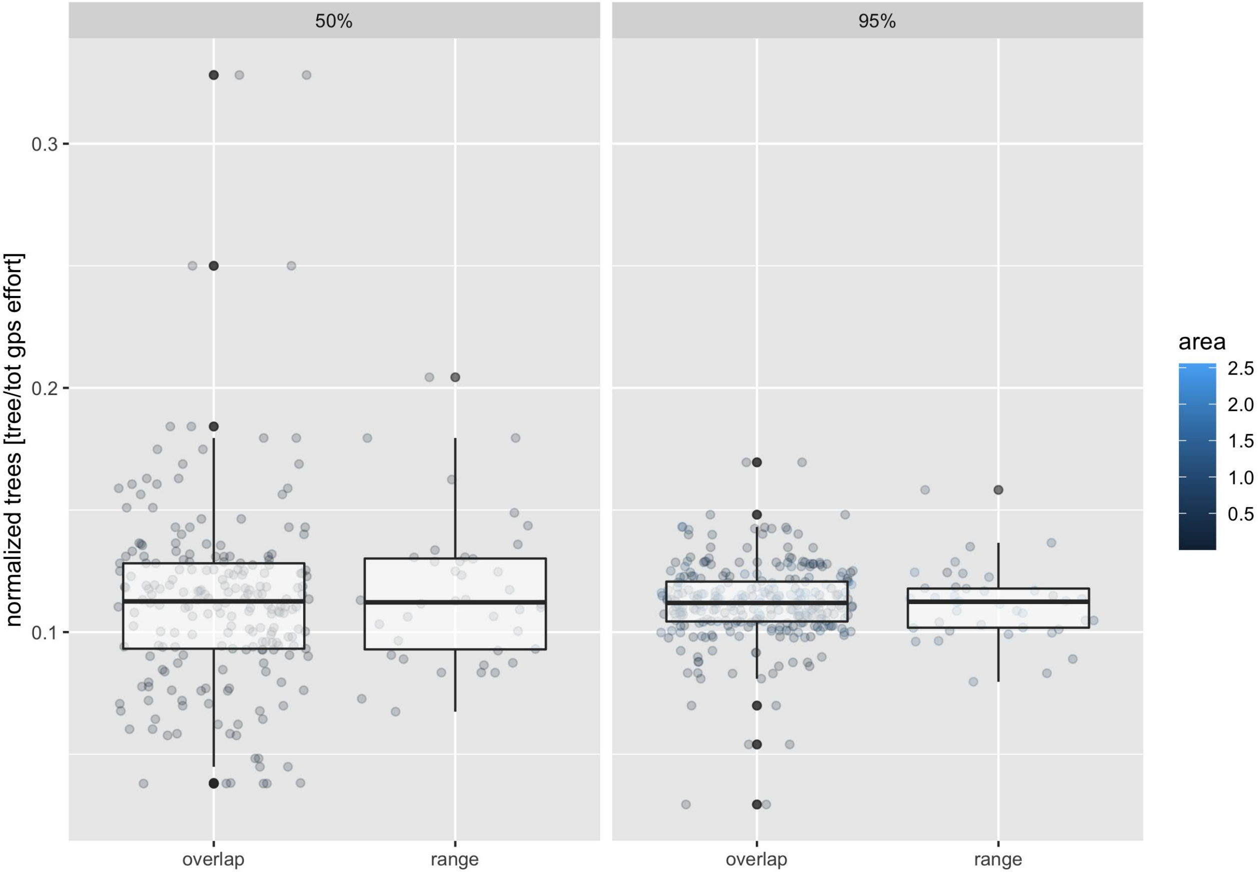


Figure 4.17 – Comparison of normalised fruit tree values for core ranges and full home ranges as well as overlaps of each delineation.

4.3 Discussion

The following discussion only relates to adult female orangutans if not mentioned otherwise and rests on the results of the analysis of the selected ten female orangutans (Chapter 4).

4.3.1 Methodology and implications

Of the ten individuals that were analysed, not all showed a clear stabilisation of their home range over the study period, but at least 4 individuals clearly showed a stable home range. The general description of site fidelity and the repeated observation of stable home ranges

in other studies shows that the concept of home range as defined in Section 4.1.1 applies to female orangutans (Ashbury, 2013; Singleton and Van Schaik, 2001; Wartmann, 2008).
In my study I found HR overlap durations of around one month when using the semivariograms and the movement models used for the AKDE approach. This may fit the definition that the home range reflects the area which an individual is ranging in for a year and which an individual chooses to keep in a mental map. Furthermore, it is possible for an orangutan to use most of the space over the duration of a year. Nonetheless, this estimate is solely based on a movement model (from AKDE). We have no actual idea of how long it actually takes until a female orangutan visits most of its home range.

Looking at the possible temporal shifts and the change of HR size over the 10 years of observation (Figure 4.6), I see multiple complications when applying the home range concept to female orangutans. Even if the concept of stable home range is useful in the case of orangutans, many uncertainties and biases occur, especially when looking at absolute HR area values.

One problem is the manual sampling approach, as it leads to a bias towards the centre of the research site and to a selection of individuals that move more often within the core area of a research site. Consequently, the home ranges calculated by KDE, BRB and MCP are strongly biased by the area of research (**RQ B.2**). This means that females that have their home range located more towards the centre of the research area, tend to have bigger home ranges. This was also the case here. This effect is nothing new and was already described by Singleton and Van Schaik (2001) and Wartmann (2008). However, in this study, we tried to show how much A. the start and selection of a follow is biased by the research trail system and the study area, and B. if losing an orangutan is spatially biased (Section 2.2.3). Both showed to be a problem, although a comparison with Tuanan in Wartmann (2008) showed that the researcher bias relating to the trail system may be slightly smaller.

Arguably the biggest problem is posed by the data availability (Section 2.2.1). Home range studies of orangutans often are based on qualitative behavioural data, where additional spatial data is gathered as a side product. The focus often lies on a few individuals, which are followed far more often. Rooney et al. (1998) already stated this as the main problem for delineating home ranges from locational animal data. Wartmann et al. (2010) states that in terms of estimating home range sizes the absolute as well as the temporal sample size is crucial for finding adequate home ranges.

The results from the AKDE algorithm showed that the traditional methods, including BRB and KDE, probably underestimate the true home range size (**RQ B.2**). The usage of a spatio-temporal movement model with the AKDE may help to find more reliable HR sizes when having low sample sizes compared to traditional methods such as KDE. Which would target the above-mentioned problem of data availability for estimating home range sizes. This algorithm also overcomes the problem of the high autocorrelation in our data and the mostly associated underestimation of HR sizes (Section 4.1.3, De Solla et al. 1999 in Zehnder 2015). Nevertheless, for analysing UDs in the context of range sharing, there is no getting around large sample size and longer research periods.

The downside of using AKDE is that it smooths home ranges to a high degree, while BRB as well as KDE are actually more useful when analysing the spatial importance of different spaces or locations within the research area. The parameterisation and estimation of HR of densely sampled individuals showed to result in reliable UDs.

The two algorithms which do not oversmooth the home ranges are the KDE and the BRB. KDE showed slightly better HRE descriptor values (e.g. holes, AUC, number of polygons) but the advantage of including temporal aspects in the HR estimation by using BRB is arguably more important than the very small difference of AUC, especially when having such an autocorrelated data set and a long research period (Patterson et al., 2017) as in our case. BRB showed less holes and polygon counts because it is based on bridges. This is a further advantage when similar pathways are used frequently (Davies et al., 2017b).

Although Wartmann (2008) found that MCP in Tuanan took more sample points to achieve a stable home range than KDE, in this study home ranges for MCP stabilised with a lower sample size (Section 4.2.1). MCP was also slightly better in estimating the full home range area when sample size is very small because luckily home ranges are actually often intrinsically convex. Nonetheless, this does not mean that these home ranges are very useful for further analysis. Generally, I strongly advise against the use of MCP. Outliers have a major effect on HR sizes and the result is a polygon instead of a far more useful UD. However, for a quick first approximation especially core ranges derived by MCP may help to find ranging patterns.

Finally, I see the temporal difference of sampling individuals and the unbalanced data set as a much bigger problem than the choice of HRE. More concurrent data about all individuals could help gaining more information about each individual's home range and especially about a momentous snapshot of range use, and possible interactions and influences between individuals. Furthermore, a more balanced data set as well as an even longer research period may make the home ranges of undersampled individuals more expressive. It would also help to use core ranges instead of home ranges when comparing range use because they are less biased by sample size and the research area (Section 4.2.5).

4.3.2 Home range estimations

Home range sizes

The sizes of home ranges were much smaller than previous findings for Suaq by Singleton and Van Schaik (2001), who looked at the HR of three individuals tracked in 1994-1998 (**RQ B.1**). They showed a HR size of 6 to 8.5 km^2 (Table 1.1). Values in our study for the 100 % MCP ranged between 2.3 ± 1.13 km^2. For all applied HREs we found values between 1.6 km^2 and 3.1 km^2 over the whole study duration and for females who definitely showed a stabilising home range (Cissy, Ellie, Lisa, Friska). The core ranges of 0.5 km^2 mentioned by Singleton and Van Schaik (2001) were more similar to our results, which ranged between 0.25-1 km^2 (Cissy, Ellie, Lisa, Friska, full period). The small grid method further applied by Singleton and Van Schaik (2001) more resembled our results (Table 1.1 and Figure 4.12). One source of the difference of full home ranges between the two studies are follows which resemble large excursions by the orangutans to the eastern or north-eastern hills as well as to the south. Singleton and Van Schaik (2001) enlarged the research area for a few months and when we take the example of Ani in their paper, we find several long excursions in the north east and south of the research area. The reason behind that are potential fruiting patterns in the hills surrounding the research area in the north and east (Singleton and Van Schaik, 2001). This would have consequences when using the above described concept of home ranges in regard of time until stable home ranges are reached, but also in regard of knowledge we can gain. When reviewing the losing points in our study we find similar locations where orangutans are lost which may indicate such excursions. Generally, long excursions are not seen in our study and this results in smaller HRs, especially with the MCP method. Nonetheless, core areas and frequently used spaces are lying within the research area and such excursions seem to be very rare (Singleton and Van Schaik, 2001). Singleton and Van Schaik (2001) even mentions that orangutans on excursions followed topographical features (hill tops, ridges) and they seemed to not know the area well. In terms of our HR definition, these excursions would therefore be ignored (Section 4.1.1).

It is worth comparing our results to the study site in Tuanan to further discuss the range sizes. First, I will compare core ranges because they tend to be more stable and less affected by uncertainties (see Section 4.3.1). I found average values of 0.6 km_2 ($KDE_{50\%}$ BCV) whereas Wartmann (2008) found values of 0.65 km_2 ($KDE_{50\%}$ BCV) and van Noordwijk et al. (2012) even found values of 0.84 km_2 ($KDE_{50\%}$ BCV) (Table 1.1). My hypothesis that home ranges and core ranges in Suaq are bigger can therefore be rejected (**RQ B.1**). When comparing CR to HR ratios, I found values of around 27% whereas Wartmann (2008) states a slightly higher value of 33%. Smaller relative and absolute CR can be explained by the higher overall orangutan density and the higher FAI. Female passive or active competition may lead to smaller range sizes, which however poses less of a challenge to the individuals because the environment is very productive. Possibly, the higher FAI alone explains smaller HR size. Such a trend was described in Tuanan by Wartmann (2008), where CR were 0.2 km_2 during the season of high fruit availability.

The average home range size I found with the KDE (here BCV for comparison) algorithm for only the four females with the highest sample size was 2.2 km_2 ($KDE_{95\%}$ BCV), whereas van Noordwijk et al. (2012) found values of 3.3 km_2 ($KDE_{95\%}$ BCV) and Wartmann (2008) for only yearly measured HRs found a value of 2.6 km_2 ($KDE_{95\%}$ BCV). Home ranges are therefore smaller than expected and previous findings by Singleton and Van Schaik (2001) have to be interpreted accordingly. They stated that the spatial "grain“ of the mosaic forest type and the longer distances in between resulted in bigger HR areas. Given our results, we rather conclude that it is actually their intuitive explanation that low FAI leads to bigger ranges in similar habitats, which is true (Singleton et al., 2009). However, we have to consider that Suaq is a site where excursions by females happen. To what degree this influences the cognitive map that the animals keep remains unknown. Furthermore, it is still possible that habitat mosaic plays a role. For instance, Singleton et al. (2009) state that in the Gunung

Palung and Tanjung Puting sites a similarly high degree of feeding tree species patchiness is found, which leads to bigger home ranges. Looking at their home range estimates shows indeed big HRs even with the grid cell method, which was not as much pronounced in earlier studies for Suaq (Knott et al. and Singleton and Van Schaik; Table 1.1).

Influences on home range sizes

We tested if home range sizes are influenced by some external variables (**RQ B.1**). Dominance and age did not show any clear statistically significant impact on the range sizes, although the hypothesis that more dominant females can claim bigger ranges cannot be confirmed nor rejected. Scramble competition, which was hypothesised as one of the explanations for bigger home ranges in Suaq, should have resulted in a clearer effect of dominance on the range sizes, especially for core ranges, where Knott et al. (2008) described more active confrontations of females where mostly the resident females gained dominance. Similar to Wartmann (2008) it was shown that variations between focals especially for full home ranges were bigger than variations due to other effects (see random effects Section 4.2.5). Ashbury (2013) mainly sees variation on the individual level originating from reproductive phases and an early exploration phase of nulliparous females. We can confirm this result based on one younger individual. Lilly, one of the younger females, which had her first offspring in 2016 (Table C.1) did show a clear increase and decrease of its 99 % and 95 % home range before the year of 2016 (Figure 4.6). The number of follows was especially influencing the full home ranges. As described in Sections 4.3.1 and 4.2.1, core range estimates were probably more reliable than HR estimates. This leads to my recommendations of preferring core ranges for comparing sites (Section 4.3.1). Regarding normalised fruit trees we found especially an effect for core ranges. The amount of normalised fruit trees explained bigger core ranges. We are again not sure if the relation probably goes the other way that during the normalisation process bigger core ranges intrinsically result in a higher normalised fruit tree value. But a quick analysis of how the normalised fruit trees within home ranges are predicted showed that the area did not have a positive effect on the normalised fruit tree value, but even more likely a negative effect (Table C.7). Therefore, more fruit trees in core ranges indeed indicate bigger core ranges. Furthermore, the matriline of Cissy (Matrilines see C.1) showed one of the highest amounts of feeding trees within its core and home range.

With respect to the hypothesis of Singleton and Van Schaik (2001) that competition and fruit trees are the explanation for home range size I see the fruit trees as a bigger factor. However, we do not see a clear influence of patchiness of feeding trees, resulting in the alteration of bigger home ranges as movements between trees are only slightly smaller than between a random sample and for full home ranges the number of trees did not explain bigger sizes (Section 3.2.5). One explanation bringing this all together could be that our methodology of normalised fruit trees as well as the uncertainty, and coverage of the tree data may not be enough to see dominance differences claiming feeding tree spaces. Therefore, a higher amount of feeding trees allows the orangutan to again gain dominance over an area and establish bigger ranges. To overcome this problem it is important to focus more on the mapping of feeding trees and species.

4.3.3 Overlaps

Overlap estimations

Overlap indices for investigating the tolerance and sociability between individuals are valid if the calculated home ranges are reliable. The above described implications were especially important for this analysis. Temporally unequally sampled data and an unbalanced number of follows may dilute the detection of tolerance and sociability. The bias based on the research site (Section 2.2.3) plays a minor role because we are especially interested in relative values. Smaller home ranges of under-sampled individuals therefore pose a smaller problem.

Overlaps were calculated and we found a slightly lower overlap of core areas than full home ranges. However, this difference is far smaller than findings from other sites. Wartmann (2008) and van Noordwijk et al. (2012) found relative shared overlaps of home ranges of up to 40 % for unrelated and up to 60 % for related females. The discrepancy to other sites would be well explained by the higher patchiness of feeding trees and the reliability on a more complex dependency of different feeding tree species (Singleton and Van Schaik, 2001). Which indicates that indeed the used data set of feeding trees was not robust enough to reveal their patchiness (Section 4.3.2). Furthermore, we can say that range sharing is very pronounced in Suaq even for core ranges, and that orangutans in Suaq have found ways to share space without excluding individuals fully from their range. I conclude that range exclusion in Suaq may happen but on a very low level and that agnostic behaviour may describe this behaviour better than range exclusion.

Influences on home range overlaps

Most overlap indices and the more advanced ones using the UD showed that the relation of females explains the higher overlap of home ranges (**RQ B.3**). This statistical significance was less pronounced for core ranges and not all overlap indices found a clearly large overlap between related females. van Noordwijk et al. (2018) showed that relative overlaps in Tuanan were around 20 % bigger for related females (relative overlap), whereas I found a slightly smaller value of 10 % (UDOI overlap). This difference can be explained by the overall very high overlaps of home ranges in Suaq. To what degree this really shows active or passive range exclusion is debatable. First, there is evidence that females are more tolerable to related females. van Noordwijk et al. (2012) observes that agnostic behaviour is far more common between unrelated individuals. Ashbury (2013) describes that relationships and relatedness are playing an important but variable role in defining an individual's home range. Furthermore, van Noordwijk et al. (2012) found that overlap sizes do not clearly correlate with higher interaction rates of females. Bigger overlap ranges between related females could also just be the byproduct of female philopatry and site fidelity.

The result that bigger overlaps are found between larger dominance category differences is unexpected (**RQ B.3**). The reason why age or dominance differences would result in higher overlaps are unknown. Our result that a bigger dominance difference explained more fruit trees in overlaps did further contradict the theory that range exclusion simply is about resources (Section 4.2.7). I argue that relationships of females may be the key to determine in more detail how space exclusion may be determined. Home ranges in Suaq are probably a difficult tool for further studying such behaviour and I propose that positional distances of concurrent follows may shed more light on such behaviour.

Chapter 5

Conclusions

This thesis analysed the socio-spatial behaviour of *pongo abelii* based on various movement parameters and discussed the results by mainly comparing them to Tuanan (*pongo pygmaeus wurmbii*), a comparable site in Borneo. The main tools were ordered on three levels of spatio-temporal resolution (Section 1.5). On the coarsest Level 1, the DJL, the SI and the sinuosity index were the main tools for the analysis on level two and the four home range algorithms (MCP, KDE, BRB, AKDE) were the main tool for analysing movement. In the following, I give a short overview of key insights in a bullet point structure (Section 5.1), followed by the remaining problems and potential future research (Section 5.2).

5.1 Main insights and limitations

General insights

- Generally, the data set needs a lot of preprocessing, but considering the amount of information and the data gathering process, it is very clean and GPS positions seem very reliable. Home range and movement parameters are not much affected by outliers. (Section 2.2.1, 2.2.2 and Figure 2.2)
- The main tools were ordered on three levels of spatio-temporal resolution (Section 1.5). On Level 2 the DJL, the SI and the sinuosity index were the main tools for the analysis, while the four home range algorithms (MCP, KDE, BRB, AKDE) were the main tools for analysing movement on Level 1.

- Overall, the limits of our movement parameters we were interested in (**RQ A.2**) became readily apparent. The sampling rate and the unbalanced data set showed to influence many of our results (Section 3.3 and 4.3.1). Probably even more on Level 1, where HRs are more reliable on balanced, synchronous samples.

- The individual has one of the biggest influences among all analysis in my thesis. The internal state of individuals and social interaction have to be understood better. Other single effects analysed mostly showed only weak explanatory power. Likewise, Wartmann (2008) stated that seasonality patterns were always smaller than variations between individuals.

- The main reason for many of the results was seen in the overall high fruit availability. FAI did not have any clear impact on movement descriptors, as it did in other study areas. This is probably the result of ceiling effects in Suaq, where orangutans are less constrained by fruit availability. I argue that movement patterns are therefore much more influenced by social factors on a more fine-grained level (Level 3).

Insights on Level 3

- FAI, which already showed to not impact DJL in Suaq compared to Tuanan, did also not affect a change of tortuosity between trees on the analysis Level 3 (Section 3.2.5). Actually, none of the factors (rain, temperature, FAI, class of focal) explained tortuosity changes between feeding trees. Slight patchiness of feeding trees is underlined by the longer average distances of a random subset (110 m) compared to the actual tree-to-tree movements (90 m) but this difference was lower than expected.

- Orangutans daily routine did show that activity is gradual over the day. Indications of higher movements in the afternoon and before building their night nests was found for the two age classes which move longer distances (Independent immatures, flanged males)(Section 3.2.5). Unflanged males were discussed to prioritise day times where flanged males reduce their activity.

Insights on Level 2

- Orangutan movement was found to be very gradual, with few stops and few strong and fast directional movements. Hence, trajectories of orangutan movement are difficult to categorise in different behavioural types based on Speed, sinuosity or turnings (Section 1.5).

- Sampling rate showed to be partially a problem for analysing movement behaviour on Level 2 (Section 3.1.3). For further judgement in future work, the analysis will need more follows sampled at a higher temporal resolution. Generally, the focal animal follows have the big advantage that we also have observational validation of movement. General movement patterns were claimed to be well kept by the 30 min sampling regime.
- Found limitations of seeing fine-grained movements (e.g., sinuosity between trees, see Insights Level 3) and the implications of the sampling rate dependency of our movement parameters have shown that on the one hand, it is possible to find differences of socio-spatial nature as in other studies like Wartmann (2008), van Noordwijk et al. (2012) and Ashbury (2013). For instance, we showed age-sex classes to be different but less different than in Tuanan (Section 3.3.3). On the other hand, I also found that the sampling rate of 30 minutes limits us in retrieving fine-grained movement and behavioural movement changes for orangutans (**RQ A.2**).
- For movement parameters, especially the tortuosity measurements have to be evaluated carefully. I propose to only use them if it is explicitly shown that they reflect the researched behaviour, e.g., as a proxy for range competence (**RQ A.2** and Section 3.3.3).
- The DJL showed to be a reliable source of information, especially when comparing age-sex classes. We found the same larger values compared to Tuanan for all age-sex classes as already Singleton and Van Schaik (2001) did (van Noordwijk et al., 2012; Wartmann, 2008). Differences are attributed to high FAI and different reproductive strategies, especially in males. Because flanged males showed the biggest difference to Tuanan and maintain much longer DJL, arguably this even leads to changes of activity during daytime (Section 3.3.3 and see level 3). This may even lead to the observed more stable dominance hierarchies in Suaq Atmoko et al. (2009). For adult females the age of the current offspring was the sole predictor found to influence DJL positively (Section 3.2.2).
- Tortuosity seems to be higher when more fruit trees are visited, even when fruit tree

fixes are deleted from the trajectories (**RQ A.3**, Section 3.2.3). This may originate from a slightly more clumped distribution of trees (also see shorter distances between trees on level 3).

- The only internal factor which showed to correlate with higher sinuosity and straightness was the age of the current offspring of females (**RQ A.3**, Section 3.2.2). This is in contrast to Wartmann (2008), who did not find an influence of the age of the current offspring on tortuosity in Tuanan. Other internal and external factors did not have an influence on tortuosity. However, this shows us that both indices actually can reveal changes in movement patterns.
- Interestingly, none of the given weather predictors had a clear effect on the movement parameters, even when different temporal averages were used (e.g., means of weather variables over the last five days) (**RQ A.3**). This was not expected; especially rain was assumed to at least partially slow down movement on level 2. As discussed, we probably miss such stops and have to further analyse weather variables and movements (needs weather data at a higher temporal resolution) on Level 3 because orangutans compensate for stops over a day during rain events by moving more after the rain.

Insights on Level 1

- The proposed home range concept fits the species well, but the application of home ranges as an analysis tool is challenging with the available orangutan movement data sets. Unbalanced sample sizes posed the biggest uncertainty in gaining new information of socio-spatial movement behaviour on Level 1. A less impactful uncertainty for resulting home ranges was found in the bias relating to the research site (Section 2.2.3. The relative comparison of e.e. UD enables us to still gain new information, although undersampling on the edge of the research area does occur (Section 4.3.1).
- Sample sizes of around 100 follows resulted in more robust HRs, whereas core ranges already stabilise with slightly lower sample size (Section 4.2.1).
- All HREs showed their disadvantages and advantages (**RQ B.2**, Section 4.2.3) and we found robust and explainable home range sizes for all methods (Section 4.2.5). Nonetheless, products generated by MCP were less useful whereas, given our unbalanced

data set, the UDs of the KDE and the BRB showed to be more useful, especially for comparing space sharing (Section 4.3.3). AKDE, which showed a very conservative, oversmoothed home range may be helpful in retrieving a reliable home range size with low sample rates but less helpful when comparing range overlaps.

- Parametrisation of KDE showed that BCV and the REF bandwidth estimator as well as PI and SCV resulted in similar outputs (Section 4.2.3). Whereas the latter tend to undersmooth and the former tend to oversmooth home ranges. Results were not extremely different, but when comparing to other sites a difference of around 0.3 km^2 has to be considered. Likewise, the different possible behaviour of the two groups when sample size is really small has to be noted (Figure 4.6).
- Parametrisation of BRB showed to be reliable with the proposed methodology (Section 4.1.7). The variation of the main influential h_{min} parameter showed that the methodology without adjustment works (e.g., h_{min} factor of 1). The inclusion of time dependency and the advantage of not violating statistical assumptions related to spatial autocorrelation shows us that it is a good alternative to KDE.
- Home range and core range sizes for females were smaller than expected and smaller than previous findings of Singleton and Van Schaik (2001). For both comparable algorithms (MCP and KDE with BCV bandwidth estimation), we found smaller values than in Tuanan (**RQ B.1**, Section 4.3.2).
- FAI, which in Tuanan was a very dominant predictor of HR size, did not predict any changes in area. None of the other factors such as dominance (equals to age), the number of follows, or the travel distance explained a variation in home range size (**RQ B.1**). Only the newly introduced normalised fruit tree value (Section 4.1.2) showed a positive impact on core range sizes but not home range sizes (Section 4.2.4).
- Various overlap indices were tested and the usage of overlap indices which use UDs for their estimation were decided to be the most appropriate (Section 4.1.2). Mainly because the delineations of home ranges are somewhat arbitrary and the optimal delineation percentage depends on the species and the data characteristics.
- Overlaps showed to be very high. Especially, the high overlap of core ranges was

not expected (**RQ B.3**). In comparison to Tuanan, relatedness was less powerful in explaining overlap indices. Core range overlap indices were less influenced by relatedness than full home ranges (Section 4.2.6). Based on the behaviour of females showing philopatry, this result cannot intuitively be seen as higher tolerance and range sharing (Section 4.3.3). In contradiction to my hypothesis dominance differences seem to result in slightly bigger overlaps. Active or passive range exclusion is nearly impossible to reveal with the methodology and data set used in this study, especially for Suaq.

- A typical pattern of higher normalised fruit tree values in some of these derived spaces (overlaps, core ranges, home ranges) was not observed (Section 4.2.8). If there is a trend, I would argue that females show slightly higher values in core ranges (like the four most tracked females in Suaq).
- The value of fruit trees in overlaps and the overlap indices showed to be positively influenced by dominance difference (**RQ B.3**. This may show that passive range exclusion or scramble competition is much more complex. A possible explanation could be that young females which occupy bigger home ranges exhibit this kind of pattern.

5.2 Open problems and future work

This thesis gives a good overview of potential movement analyses of the the data available on orangutan movement in Suaq. Many of the hypotheses referring to my research questions had to be rejected and clearly conclusive results were not found. However, the results help to highlight which directions were dead ends, and which ones are promising avenues for future work. Furthermore, the data processing was a main part of this thesis and the resulting cleaned data sets are now ready for further use (Figure 2.2). R scripts are available for free use on my GitHub repository (`https://github.com/greentrea/SUAQr`).

Some ideas for future research, which I see as very fruitful, are the inclusion of path heights (3D) in the movement parameters because longer travel distances may also reveal that there is a different pattern of vertical movement, while so far we only focused on horizontal movement (Section 3.3.1). Furthermore, the systematic analysis concurrent follows and potential avoidance or tolerance patterns as well as leading following patterns of the mother and offspring could harbour new insights on socio-spatial aspects (e.g. relationship structures).

But in general, I see two main possibilities for future research, which I would hope to solve many of the stated problems and hopefully lead to clearer results relating to spatial movement behaviours. First, the systematic mapping of resources, e.g., feeding trees, would help in normalising the feeding tree data set. I argue that these are important spaces for orangutans and that daily movement and ranging does react to the underlying patterns of the habitat. Furthermore, we would be able to compare if there is indeed a higher patchiness of important feeding trees, leading to bigger DJL, or if they are mainly the result of the actual abundance of fruit availability and therefore the easier energy intake.

Second, on Level 1, a balanced data set spanning at least one or two month would help immensely to overcome the described biases in estimating home ranges and investigating the drivers of range tolerance or competition, respectively (Section 4.3.1). A desirable follow of multiple individuals over a longer period would reveal a direct reaction to each other and passive or active range exclusion as well as tolerance would be better visible. Creative tracking and following approaches are required because disturbances of individuals still have to be minimised. Possibly drones or other digital tools might help in the future.

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Appendices

Appendix A

Appendix: Data preparation and general methodology

A.1 Mean observation duration

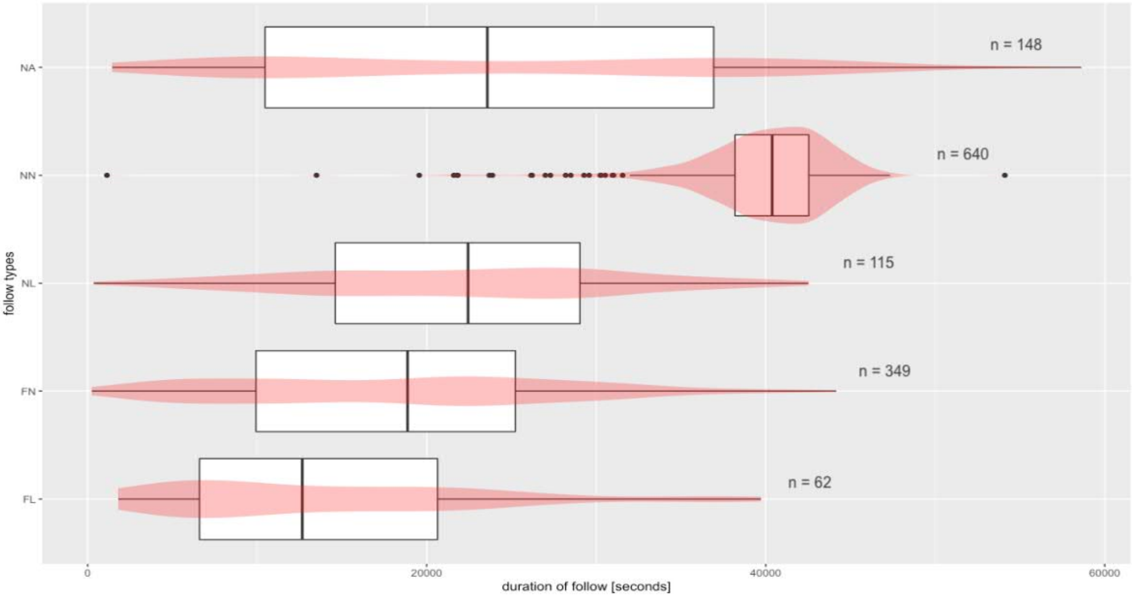


Figure A.1 – Box plot of the different follow types if available and the corresponding follow duration. A violin plot was overlaid to show the distribution density.

T

A.2 Orangutan spatial data

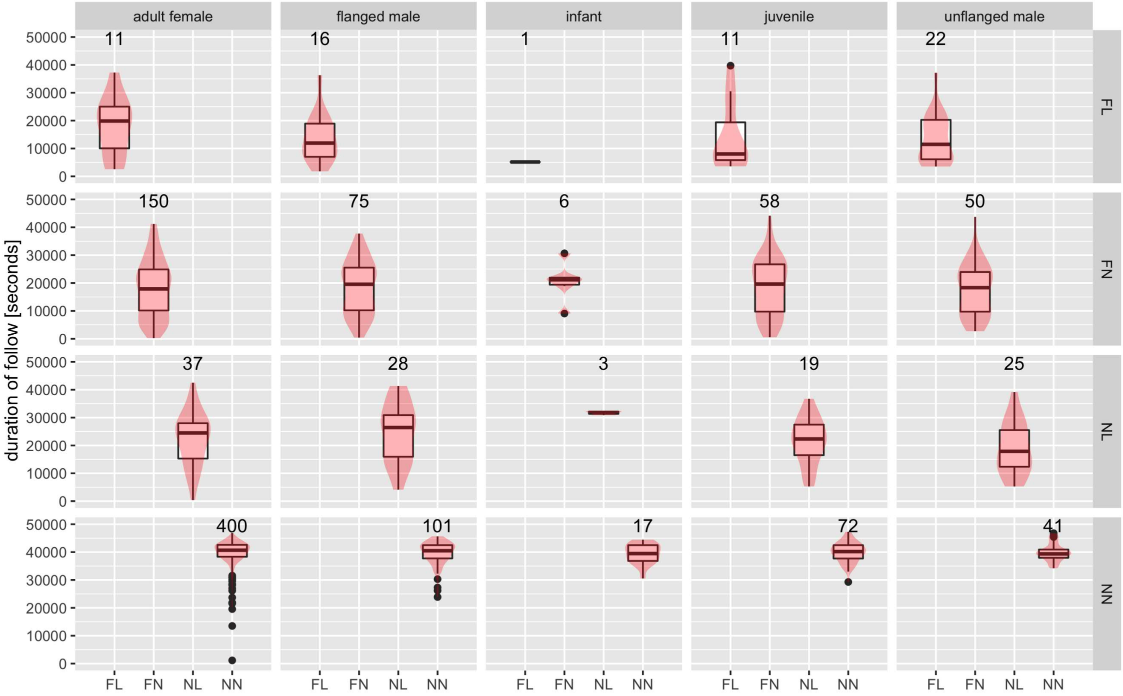


Figure A.2 – Box plot of the different follow types (without NA's) and focal class and the observed duration for their follows. An an analysis of variance (ANOVA) of the observation duration of the focal age class groups suggest that there is no difference between age class groups (F(4,626) = 0.251, p = .909).

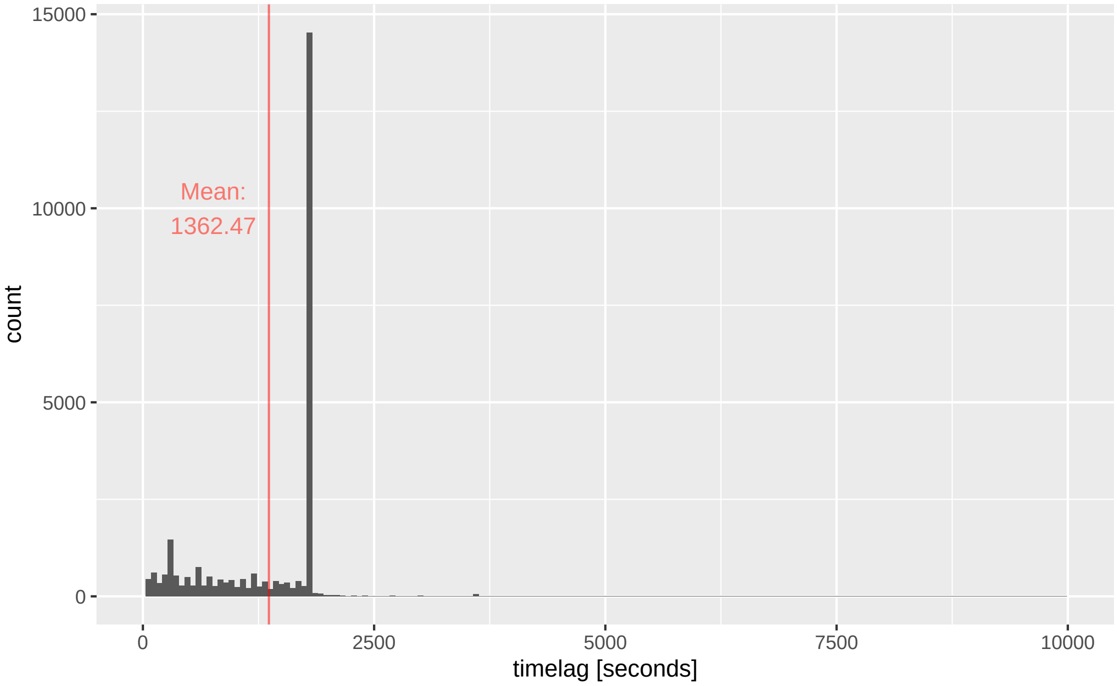


Figure A.3 – The 30 min sampling regime is clearly observable with few shorter sampling intervals and rare larger sampling intervals. Two third of all GPS-fixes (58%) have a time lag of 1800 seconds (30 min) to the last GPS-fix. When filtering out tree-points this number further increases to 65%. So the sampling interval is quite reliable. When including all shorter sampling intervals which are mostly the last and first steps between morning nests and the first 30 min ranging point (+35%) and including all steps with a time lag below 1 hour (+2%) (so if one point was accidentally skipped) we already get ca. 95% of the data.

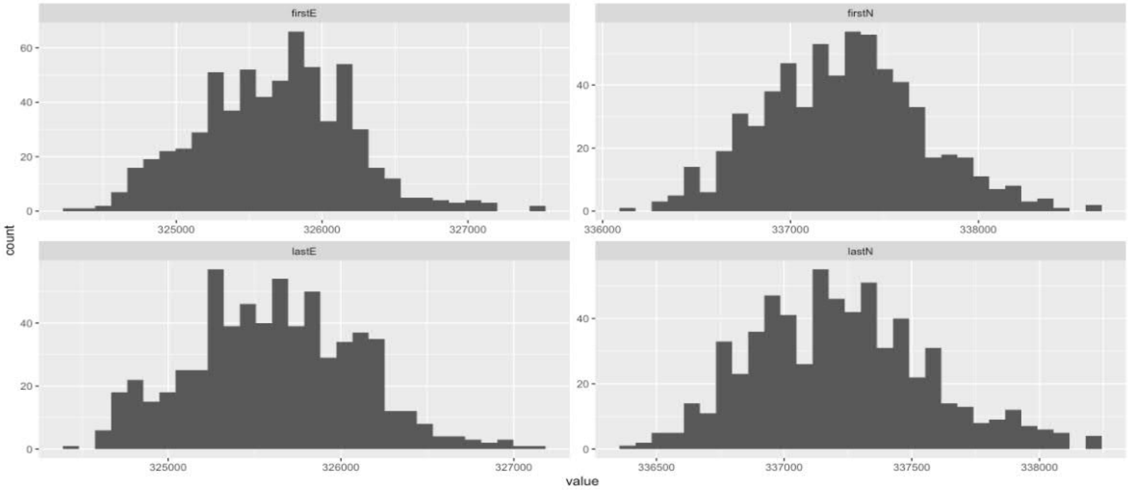


Figure A.4 – The values of easting, northing for start and end po points is pretty normally distributed over the research area with a slight bias or skewness towards the southwestern area where the research station is located.

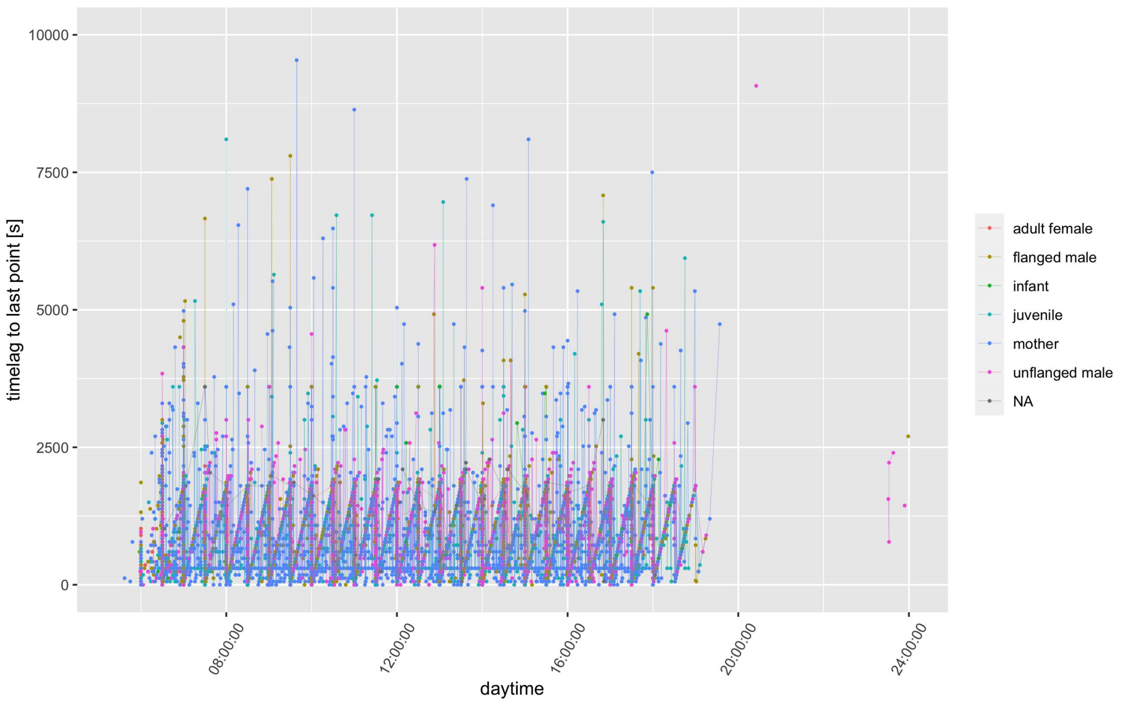
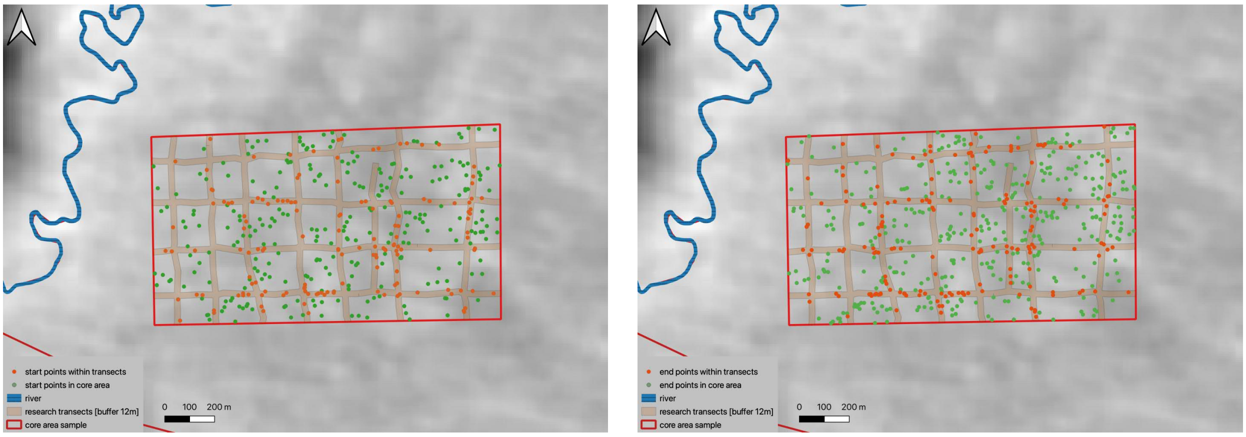


Figure A.5 – Measured sampling intervals between GPS-fixes over the course of a day. The sampling interval equals to the time to the next GPS-location. It can be assumed that such shorter and longer GPS intervals occur equally over the day with few outliers in the evening/night. Shorter sampling intervals which are originating from additional points to the 30 min sampling regime result in the zigzag pattern. Furthermore the 1800 second line as well as the 3600 second line (where a 30 min point was probably missed) is visible.

A.3 Researcher bias



(a) start points **(b)** end points

Figure A.6 – Comparing end and start points within the buffered research transects to the total within the core area.

A.4 Weather and fruit availability.

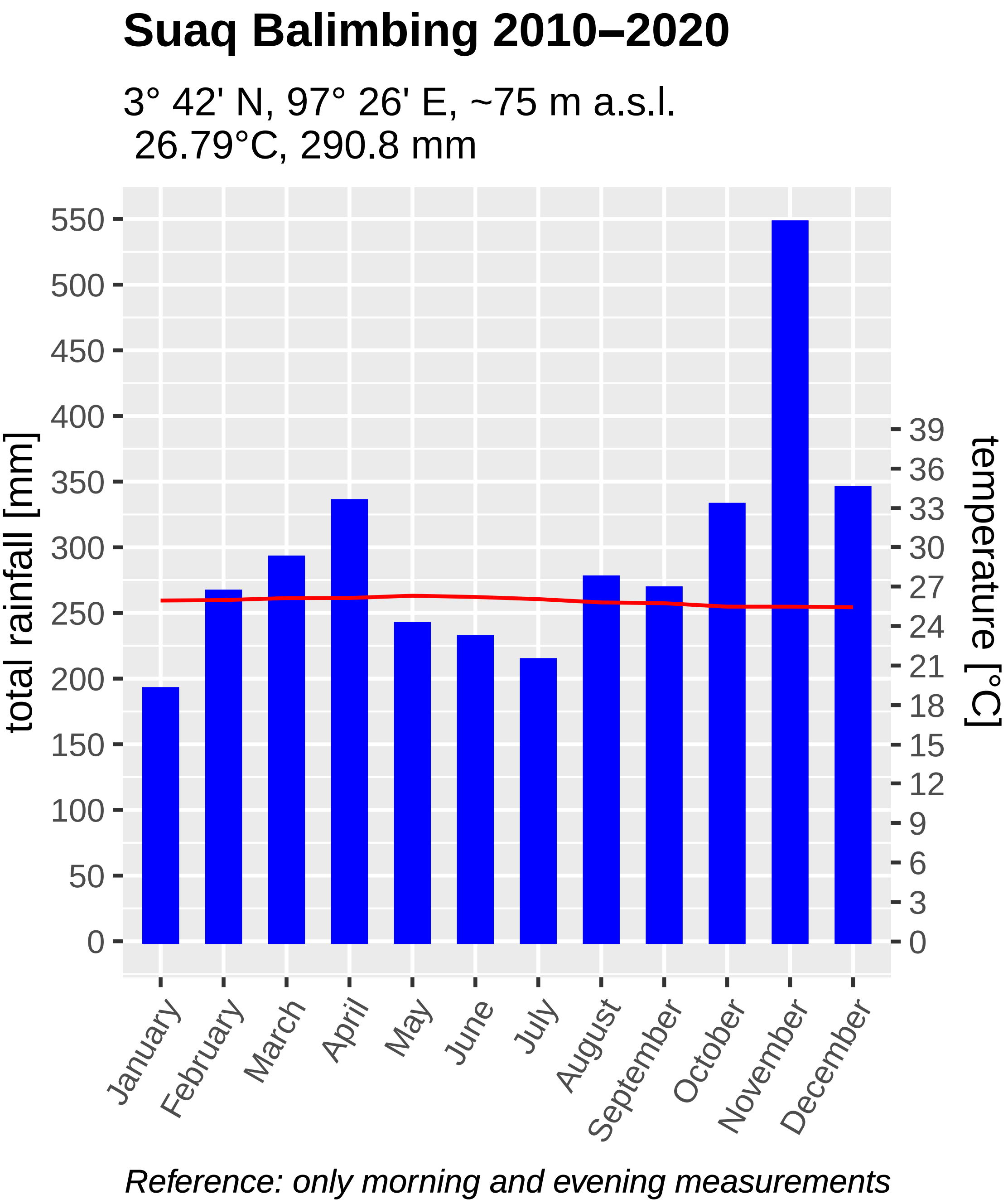


Figure A.7 – Precipitation and temperature for Suaq Balimbing. Temperatures and precipitation are significantly different for months October, November and December although the temperature stays very stable over time. If we would zoom in at the mean temperatures we would clearly see differences between the end of the year and the rest of the months.

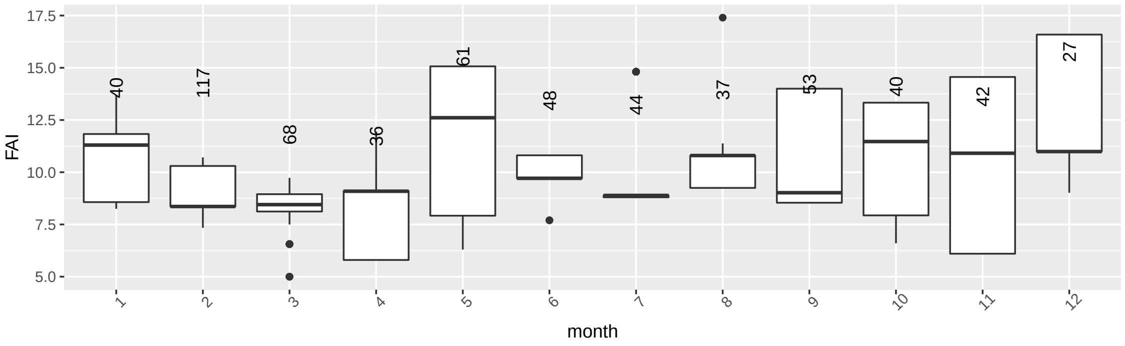


Figure A.8 – Difference of FAI during the year. The mean FAI for all months was 9.7 with a minimum of 3.4 and a maximum of 18.27. No month was significantly different from the general mean (Kruskal-Wallis, df = 11,$\tilde{\chi}^2$ = 10.66, p = 0.47).

Appendix B

Appendix: Movement

B.1 Background and methods

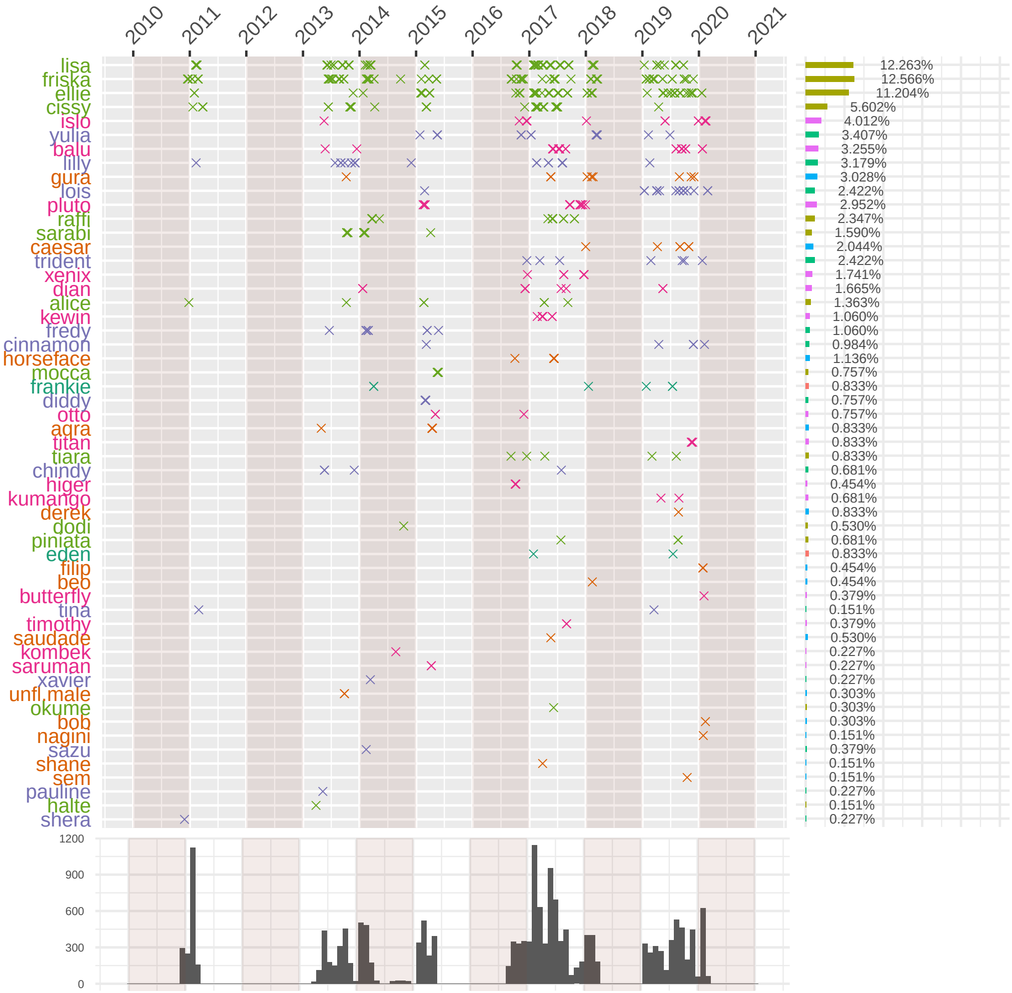


Figure B.1 – All individuals tracked and their corresponding sampling effort.

B.1.1 Movement parameters

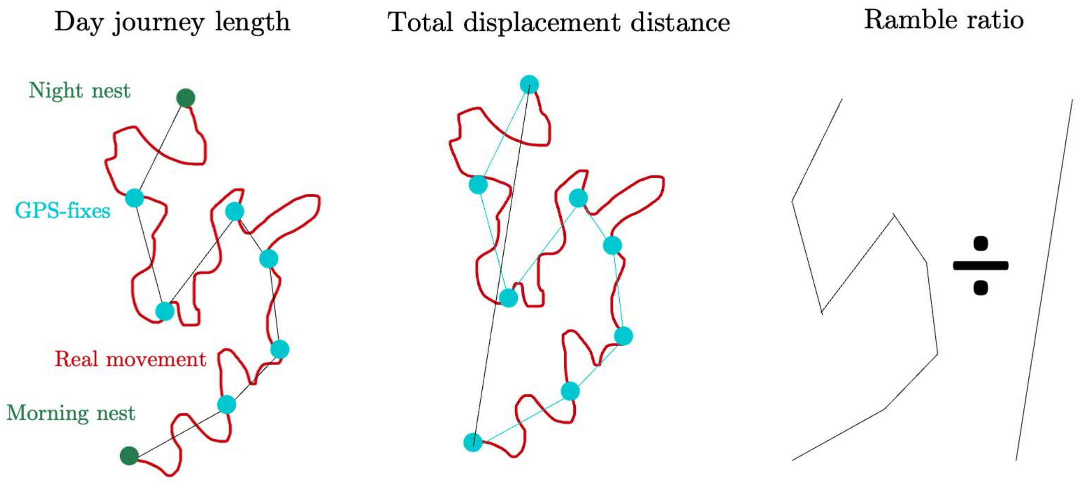


Figure B.2 – Visualisation of the different movement parameter of DJL, the TDD and the derived RR

B.1.2 Movement between feeding trees

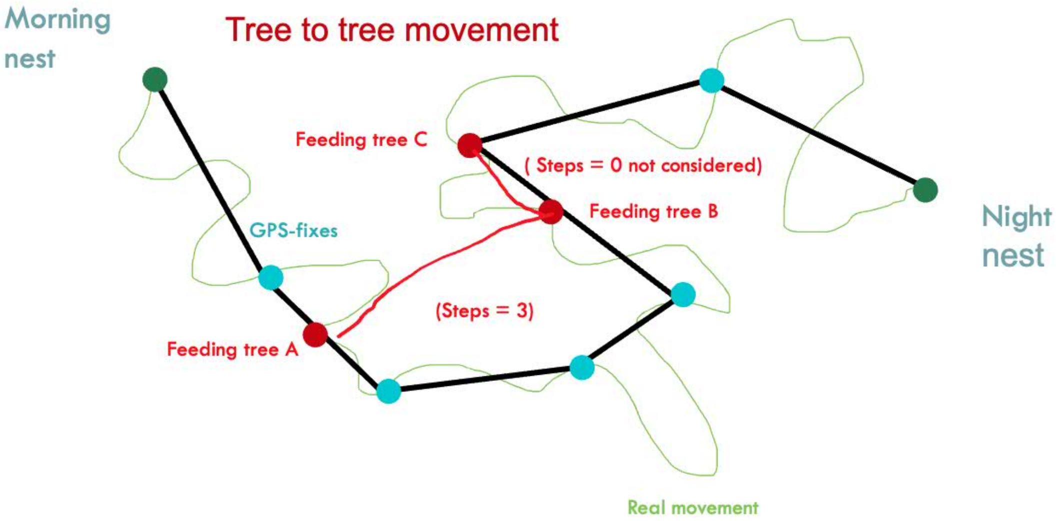


Figure B.3 – Explanation of the derived statistics for the tree A to tree B movement.

B.2 Results and discussion

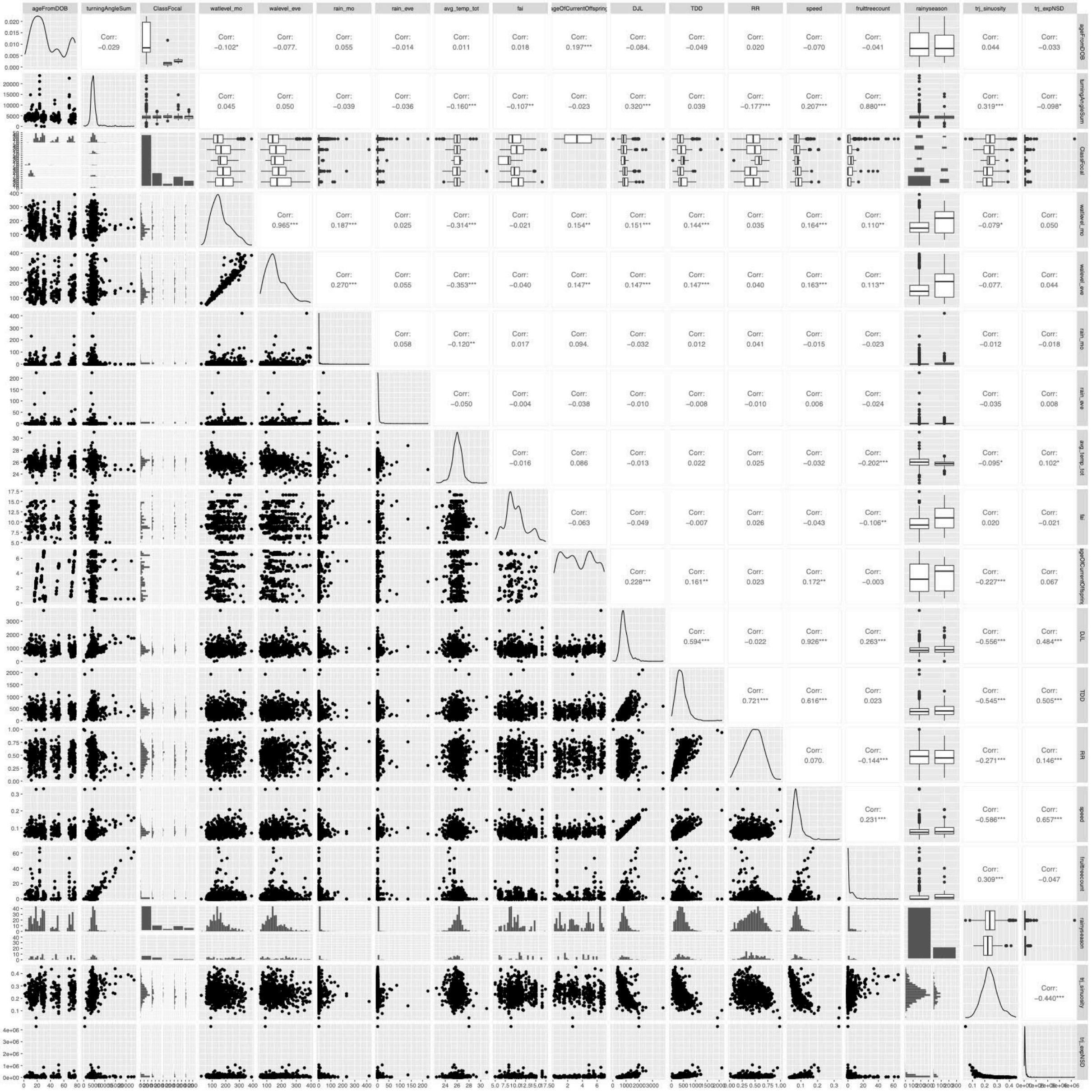
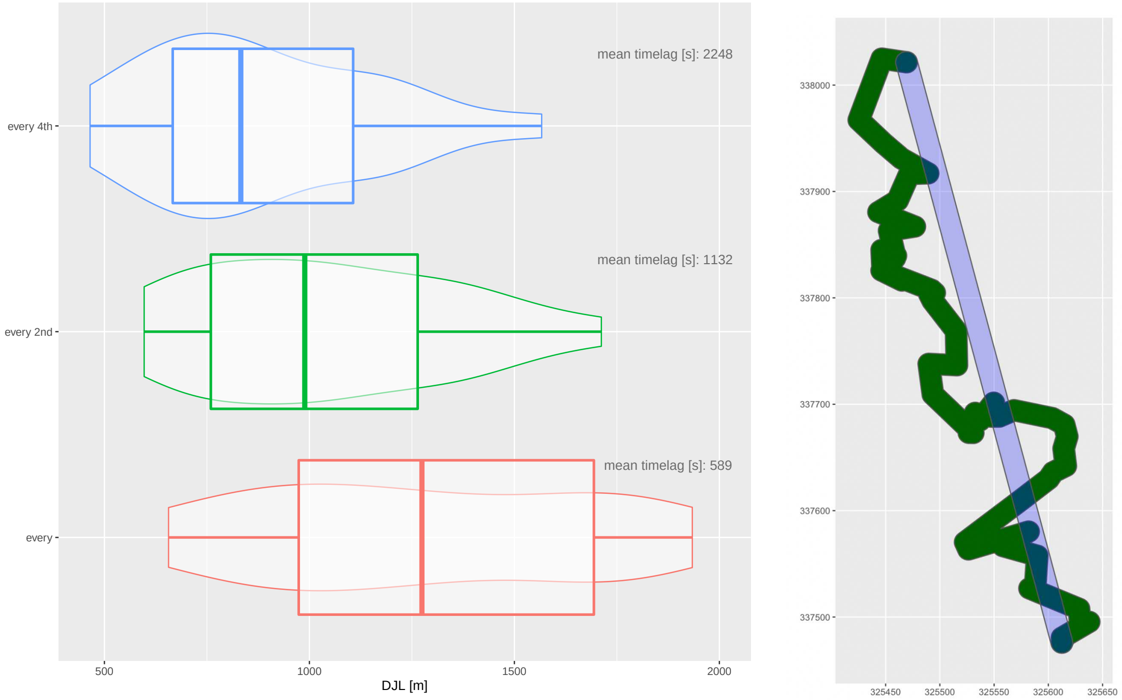


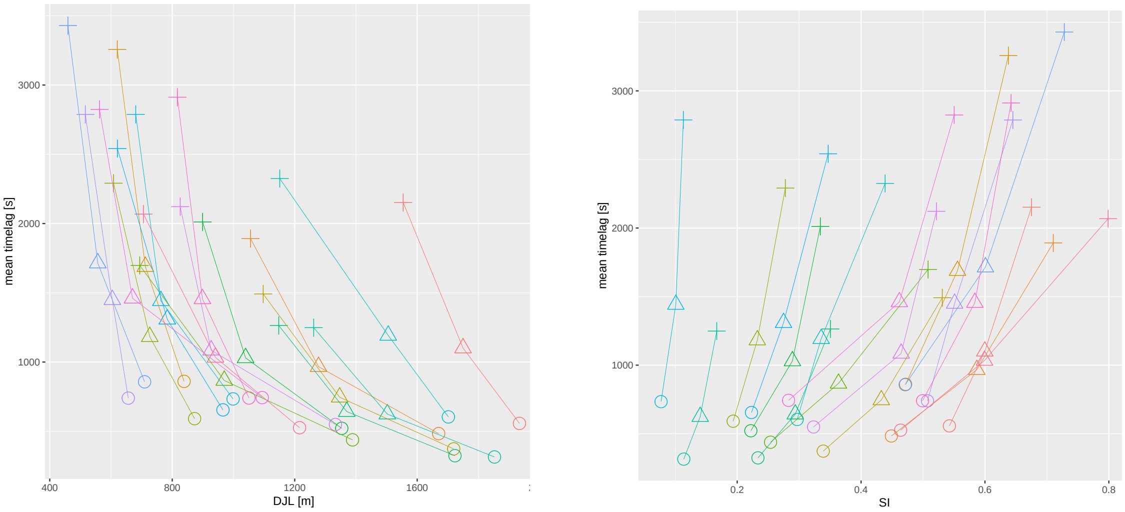
Figure B.4 – Scatterplot matrix of movement parameter and explanatory variables.

B.2.1 Uncertainties in movement parameter

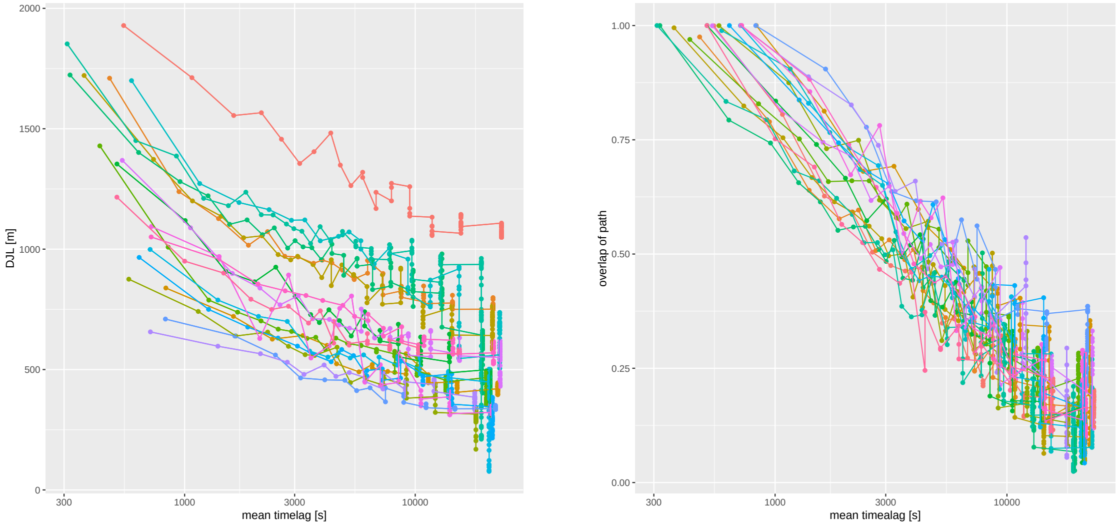


(a) subsampled follow **(b)** overlap

Figure B.5 – **(a)** Distribution of each subsampling group. The mean time lags for the subsampled follows is also indicated in seconds. We see that the sampling regime changed from an average of ca. 10 min to 20 min for every second GPS fix and to ca. 40 min for every fourth GPS fix. **(b)** The area under the subsampled movement path (dark blue green) when the path is fully subsampled (start-end). This was done for every subsample possible (every 2^{nd},3^{rd}... until only start and end points remained)



(a) DJL (triangle = every 2nd, cross = every 4th) **(b)** SI (triangle = every 2nd, cross = every 4th)



(c) subsampling bootstrap DJL **(d)** subsampling bootstrap path overlap

Figure B.6 – **(a)** The visualisation of the development of the corresponding DJL. **(b)** The visualisation of the development of the corresponding SI. We see that DJL is negatively affected by reducing the sampling frequency and straightness is positively influenced. The differences between individual follows more or less stayed the same independently of the sampling scheme. **(c)** The results of bootstrapping the whole trajectory where every possible subsampling frequency was applied (every 2nd,3rd)... until only start and end points remained). The pattern remained similar to the three initial subsampling frequencies but it becomes more obvious that above 40 minutes the trajectories are getting unstable. **(d)** The overlap area of the original trajectory (buffered: 10 m) with the subsampled trajectories (buffered: 10 m) was calculated and given in percentage to the original trajectory area. Here it becomes even more obvious that for longer intervals than 40 minutes the overlap is increasingly fluctuating. Mean overlap compared to the original trajectory for a sampling rate of around 30 minutes is 74±3%.

B.2.2 Movement parameters

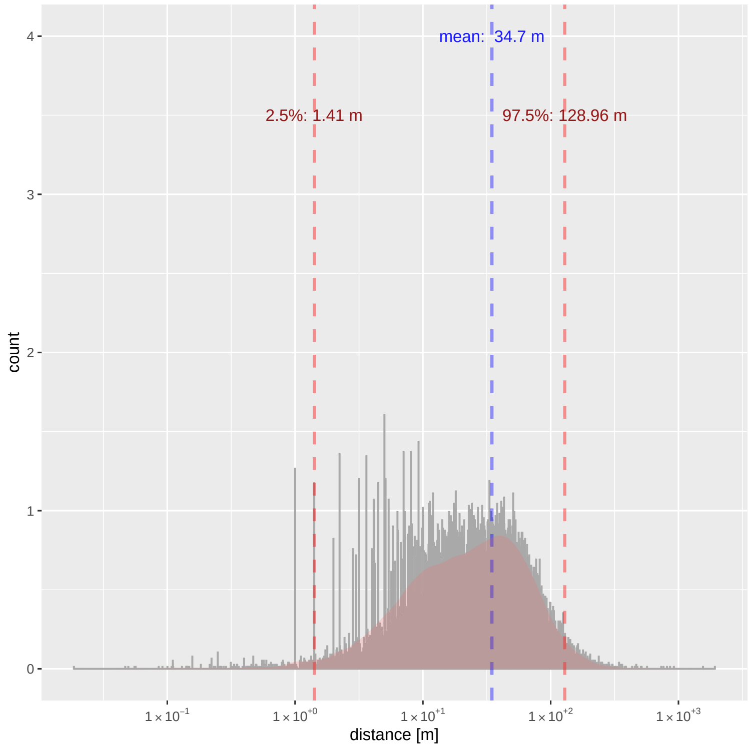


Figure B.7 – Distribution of edge lengths.

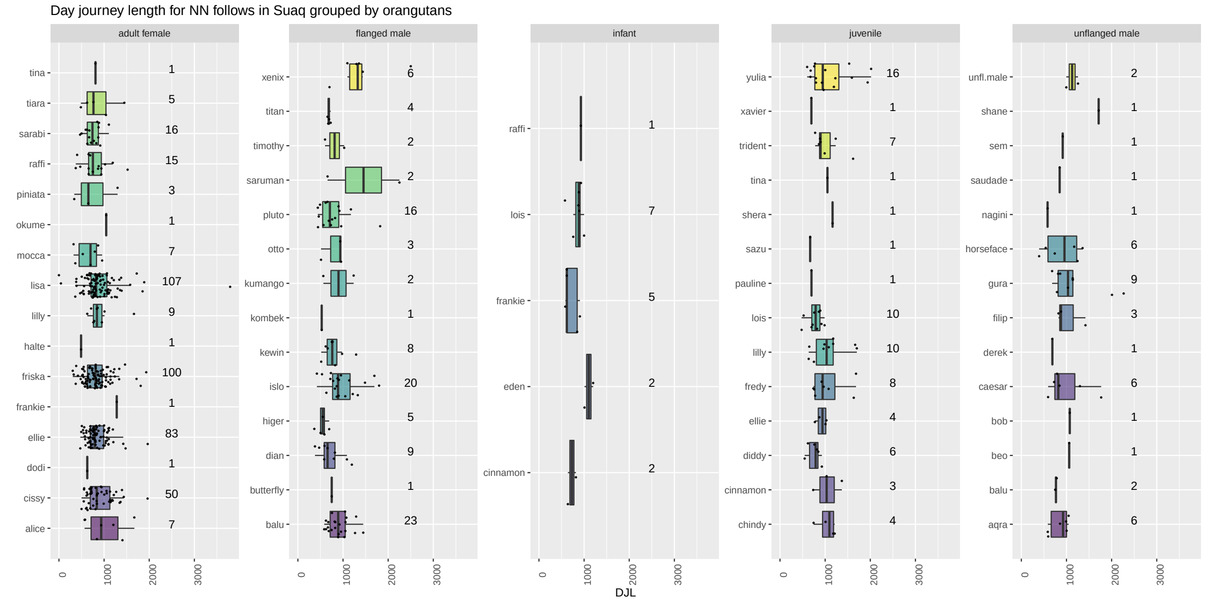
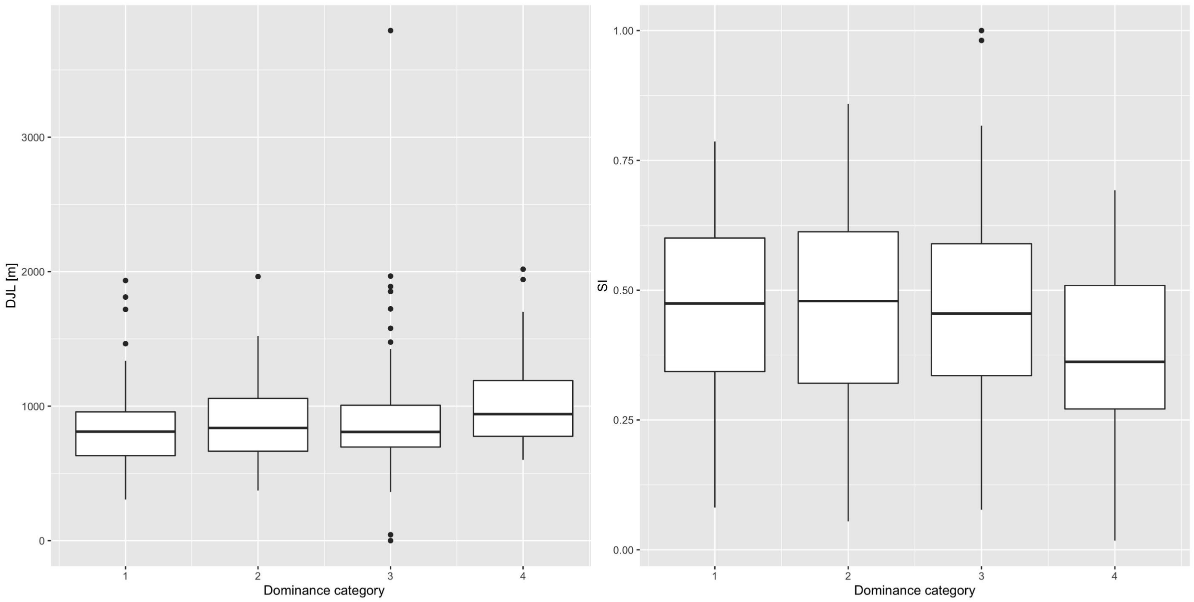


Figure B.8 – Overview of DJL for every indivdual per age-sex class.

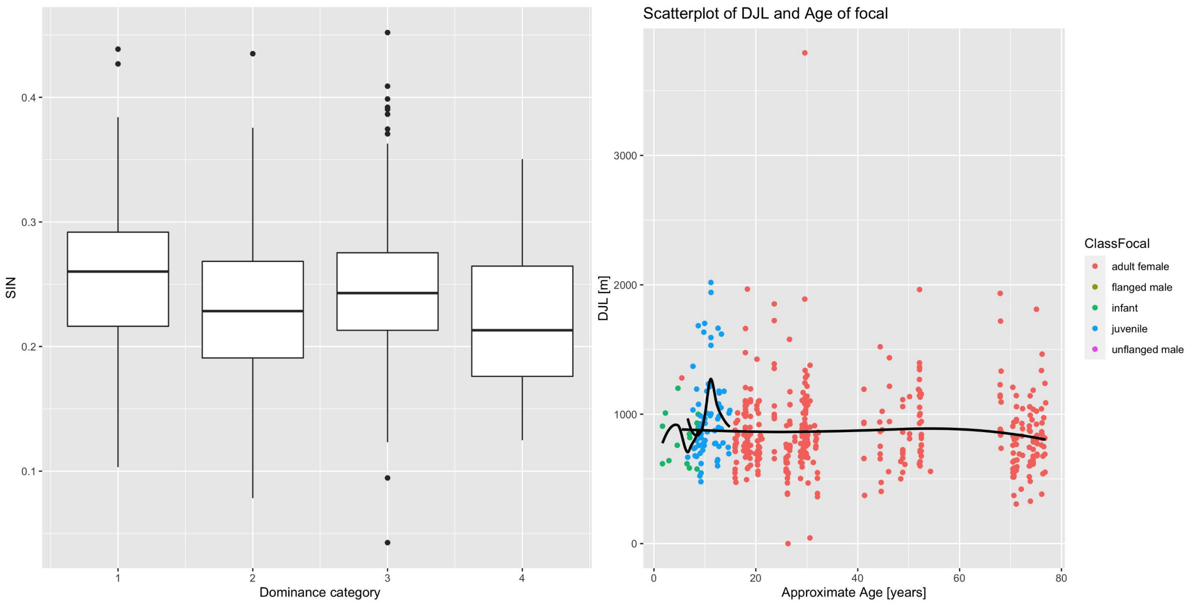
Table B.1 – Overview of day journey length.

focal	class	# follows	age	offsp. age	DJL*	TDD*	SI	sinuosity	speed**	length	turn angle***	trees	points	sampling interv.
aqra	unflanged male	6	independent	independent	847±208	366±269	0.4±0.25	0.21±0.05	0.083±0.25	10:14:30	3576	0	22.3	00:28:52
balu	unflanged male	2	independent	independent	767±25	427±39	0.56±0.07	0.22±0.02	0.068±0.07	11:18:30	4353	0	24.5	00:28:53
beo	unflanged male	1	independent	independent	1060±NA	319±NA	0.3±NA	0.23±NA	0.085±NA	12:26:00	4791	0	27	00:28:42
bob	unflanged male	1	independent	independent	1073±NA	725±NA	0.68±NA	0.19±NA	0.103±NA	10:24:00	3593	9	31	00:20:48
caesar	unflanged male	6	independent	independent	1004±445	451±205	0.45±0.09	0.25±0.07	0.091±0.09	11:07:30	5010	5	29.8	00:23:16
derek	unflanged male	1	independent	independent	688±NA	59±NA	0.09±NA	0.35±NA	0.053±NA	13:00:00	6039	4	32	00:25:10
filip	unflanged male	3	independent	independent	1041±331	612±308	0.57±0.1	0.25±0.1	0.097±0.1	10:53:00	5218	8	32	00:21:37
gura	unflanged male	9	independent	independent	1193±562	483±266	0.42±0.19	0.2±0.04	0.104±0.19	11:21:07	4290	1	26.9	00:26:34
horseface	unflanged male	6	independent	independent	908±403	554±351	0.57±0.16	0.24±0.08	0.082±0.16	11:02:40	4335	1	26.3	00:26:14
nagini	unflanged male	1	independent	independent	581±NA	342±NA	0.59±NA	0.33±NA	0.059±NA	09:47:00	4892	8	29	00:20:58
saudade	unflanged male	1	independent	independent	849±NA	343±NA	0.4±NA	0.22±NA	0.071±NA	12:01:00	5426	2	29	00:25:45
sem	unflanged male	1	independent	independent	917±NA	628±NA	0.69±NA	0.21±NA	0.088±NA	10:25:00	4802	7	31	00:20:50
shane	unflanged male	1	independent	independent	1713±NA	959±NA	0.56±NA	0.13±NA	0.136±NA	12:35:00	5198	0	27	00:29:02
unfl.male	unflanged male	2	independent	independent	1126±183	209±24	0.19±0.05	0.17±0.01	0.102±0.05	11:00:00	3906	0	24	00:28:42
chindy	independent immature	4	11.6	independent	1036±214	620±262	0.58±0.18	0.16±0.04	0.098±0.18	10:41:15	4016	0	22.5	00:29:47
cinnamon	independent immature	3	7.7	independent	1046±318	387±171	0.37±0.09	0.24±0.04	0.096±0.09	10:57:40	5755	9	32.7	00:20:53
diddy	independent immature	6	9.2	independent	753±144	252±72	0.34±0.09	0.27±0.06	0.066±0.09	11:25:00	3757	0	25.2	00:28:22
ellie	independent immature	4	13.4	independent	921±121	445±238	0.47±0.21	0.25±0.07	0.082±0.21	11:12:30	5852	12	35.5	00:23:03
fredy	independent immature	8	9.1	independent	1070±382	455±264	0.42±0.19	0.22±0.05	0.092±0.19	11:38:00	3942	0	25.2	00:28:50
lilly	independent immature	10	12.5	independent	1079±374	471±142	0.46±0.13	0.21±0.05	0.096±0.13	11:04:54	4894	4	30.2	00:25:42
lois	independent immature	10	9.2	independent	766±166	436±159	0.56±0.17	0.26±0.06	0.078±0.17	09:45:42	4342	6	27.7	00:22:19
pauline	independent immature	1	independent	independent	697±NA	273±NA	0.39±NA	0.26±NA	0.061±NA	11:22:00	4041	0	25	00:28:25
sazu	independent immature	1	6.6	independent	668±NA	327±NA	0.49±NA	0.24±NA	0.068±NA	09:53:00	3065	0	23	00:26:57
shera	independent immature	1	12.8	independent	1164±NA	538±NA	0.46±NA	0.11±NA	0.101±NA	11:29:00	3657	4	18	00:40:32
tina	independent immature	1	13.2	independent	1051±NA	525±NA	0.5±NA	0.27±NA	0.087±NA	12:08:00	10125	27	60	00:12:20
trident	independent immature	7	12.1	independent	1038±294	493±188	0.48±0.1	0.23±0.06	0.092±0.1	11:16:51	5014	5	30	00:23:35
xavier	independent immature	1	14.7	independent	695±NA	274±NA	0.39±NA	0.26±NA	0.055±NA	12:37:00	4553	0	27	00:29:07
yulia	independent immature	16	10.3	independent	1093±453	251±128	0.26±0.14	0.22±0.07	0.093±0.14	11:36:22	4649	2	28.2	00:26:01
cinnamon	infant	2	5	independent	730±126	420±76	0.59±0.21	0.22±0	0.078±0.21	09:20:00	3132	2	21.5	00:27:42
eden	infant	2	3.5	independent	1105±135	534±50	0.49±0.11	0.2±0.05	0.091±0.11	12:07:30	4748	7	34	00:22:03
frankie	infant	5	4.7	independent	715±151	323±186	0.43±0.2	0.29±0.06	0.062±0.2	11:29:36	4581	4	28.6	00:25:23
lois	infant	7	8	independent	845±138	522±97	0.62±0.06	0.25±0.03	0.079±0.06	10:44:09	4898	5	28.7	00:23:38
raffi	infant	1	41.2	independent	929±NA	730±NA	0.79±NA	0.18±NA	0.09±NA	10:20:00	3361	0	22	00:29:31
balu	flanged male	23	independent	independent	903±231	461±180	0.52±0.17	0.24±0.05	0.082±0.17	11:06:47	4708	3	27.2	00:25:52
butterfly	flanged male	1	independent	independent	749±NA	70±NA	0.09±NA	0.29±NA	0.065±NA	11:30:00	5018	8	34	00:20:55
dian	flanged male	9	independent	independent	731±272	238±123	0.33±0.13	0.27±0.08	0.066±0.13	11:01:40	4319	3	27	00:25:40
higer	flanged male	5	independent	independent	540±121	231±118	0.43±0.19	0.31±0.07	0.057±0.19	09:33:12	3568	4	24.8	00:24:23
islo	flanged male	20	independent	independent	986±364	549±317	0.53±0.21	0.24±0.06	0.088±0.21	11:12:27	4995	5	29.4	00:24:04
kewin	flanged male	8	independent	independent	801±242	440±220	0.53±0.14	0.26±0.07	0.068±0.14	11:47:52	4328	0	25.8	00:28:37
kombek	flanged male	1	independent	independent	528±NA	296±NA	0.56±NA	0.27±NA	0.05±NA	10:32:00	3414	0	23	00:28:44
kumango	flanged male	2	independent	independent	900±475	453±199	0.52±0.05	0.26±0.12	0.088±0.05	10:10:00	4698	4	26.5	00:23:55
otto	flanged male	3	independent	independent	803±252	405±315	0.44±0.31	0.23±0.11	0.077±0.31	10:56:40	3538	0	23.7	00:28:53
pluto	flanged male	16	independent	independent	779±349	387±208	0.48±0.17	0.24±0.06	0.071±0.17	10:54:30	4102	1	24.6	00:28:00
saruman	flanged male	2	independent	independent	1454±1126	1256±1208	0.77±0.23	0.18±0.11	0.132±0.23	10:59:00	4066	0	23.5	00:29:18
timothy	flanged male	2	independent	independent	814±300	558±107	0.71±0.13	0.19±0	0.093±0.13	08:41:30	3551	0	20	00:27:39
titan	flanged male	4	independent	independent	687±30	233±38	0.34±0.06	0.26±0.02	0.066±0.06	10:33:30	5176	4	28.2	00:23:17
xenix	flanged male	6	independent	independent	1398±601	527±220	0.39±0.17	0.19±0.05	0.121±0.17	11:32:40	4209	0	26.2	00:27:37
alice	adult female	7	independent	2	1030±417	511±298	0.48±0.2	0.25±0.08	0.088±0.2	11:36:09	6045	6	35	00:25:11
cissy	adult female	50	50.8	3.9	905±296	402±231	0.45±0.2	0.22±0.06	0.083±0.2	10:51:25	4391	1	26	00:27:19
dodi	adult female	1	31.3	independent	627±NA	267±NA	0.43±NA	0.28±NA	0.054±NA	11:42:00	3800	0	25	00:29:15
ellie	adult female	83	18.6	2.9	841±237	425±241	0.5±0.17	0.25±0.05	0.075±0.17	11:25:53	4619	3	28.8	00:25:09
frankie	adult female	1	5.5	independent	1280±NA	704±NA	0.55±NA	0.21±NA	0.12±NA	10:41:00	5655	10	35	00:18:51
friska	adult female	100	72.8	3.9	831±291	377±171	0.46±0.17	0.25±0.07	0.075±0.17	11:03:42	4741	4	29	00:26:27
halte	adult female	1	independent	independent	490±NA	235±NA	0.48±NA	0.25±NA	0.056±NA	08:46:00	3324	0	19	00:29:13
lilly	adult female	9	16.4	1.4	912±304	368±221	0.39±0.13	0.24±0.06	0.082±0.13	11:07:20	4514	2	27.2	00:25:57
lisa	adult female	107	28.5	4.2	900±417	395±215	0.45±0.19	0.24±0.07	0.083±0.19	10:55:50	5080	5	30.3	00:25:10
mocca	adult female	7	independent	independent	648±248	354±264	0.47±0.25	0.3±0.1	0.06±0.25	10:45:51	3618	0	23.9	00:28:17
okume	adult female	1	independent	independent	1047±NA	335±NA	0.32±NA	0.26±NA	0.082±NA	12:47:00	5027	1	31	00:25:34
piniata	adult female	3	independent	independent	763±489	319±169	0.44±0.05	0.25±0.03	0.074±0.05	09:43:20	3415	1	21.7	00:28:32
raffi	adult female	15	43.4	independent	802±304	396±172	0.49±0.12	0.25±0.08	0.077±0.12	10:22:44	4012	0	23.5	00:27:50
sarabi	adult female	16	29.1	0.9	749±169	273±104	0.37±0.14	0.25±0.05	0.065±0.14	11:32:19	4057	0	25.8	00:28:06
tiara	adult female	5	independent	independent	873±382	533±343	0.58±0.29	0.22±0.09	0.078±0.29	11:09:48	4882	1	25.8	00:27:05
tina	adult female	1	21.2	independent	810±NA	371±NA	0.46±NA	0.23±NA	0.079±NA	10:16:00	4427	4	24	00:26:47

*: [m], **: [km/h], ***: [°]



(a) dominance and DJL **(b)** dominance and SI



(c) dominance and sinuosity **(d)** age of the focal and DJL

Figure B.9 – Influence of age and dominance on DJL. Age and dominance correlated highly therefore the results can be seen interchangeably (maximum age is 77 therefore a the change per category is around 20 times less per year than per dominance category). All effects were not statistically significant in the model.

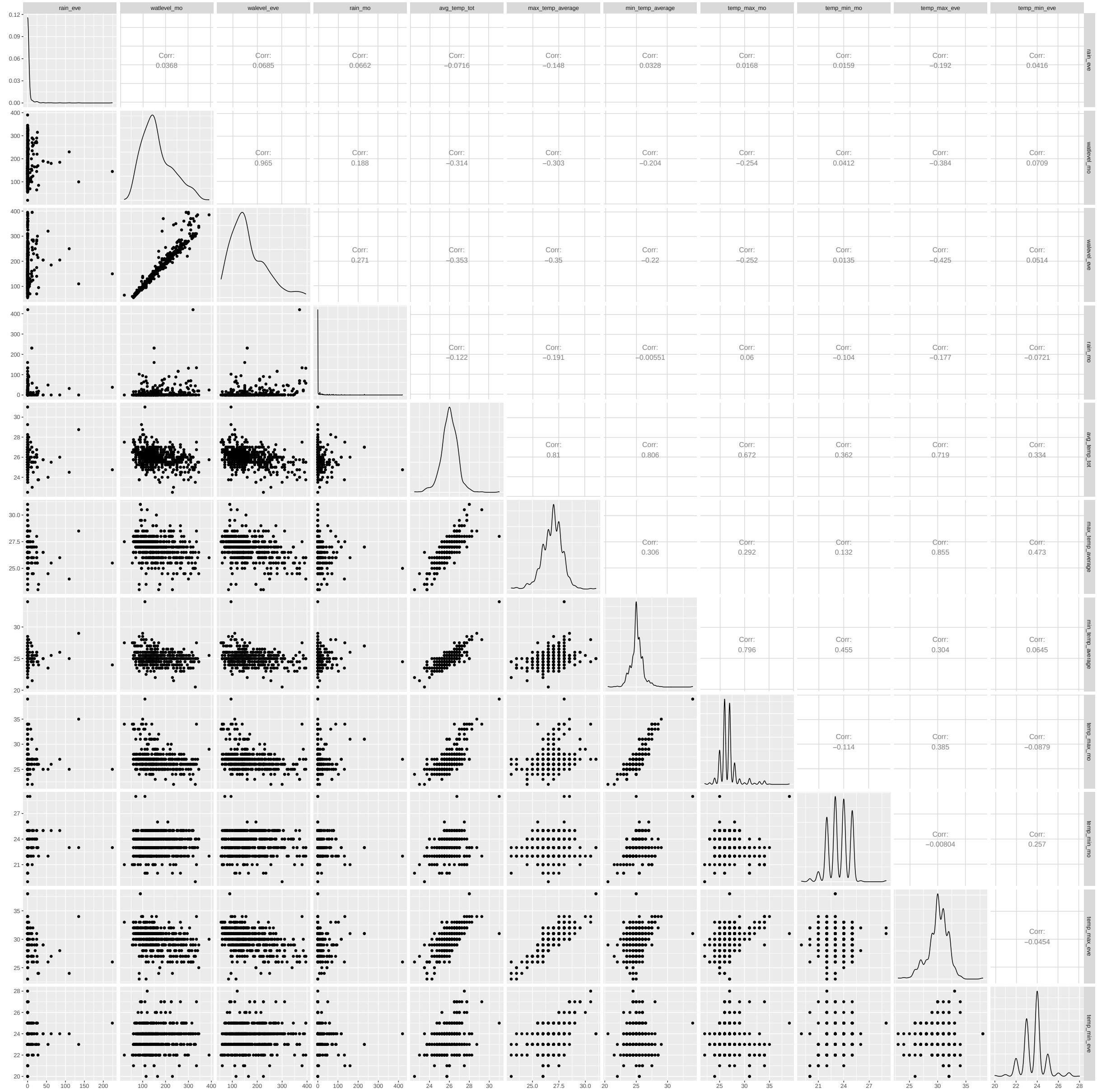


Figure B.10 – The colinearity of weather variables posed a problem and key weather variables based on their correlation and expected expressiveness.

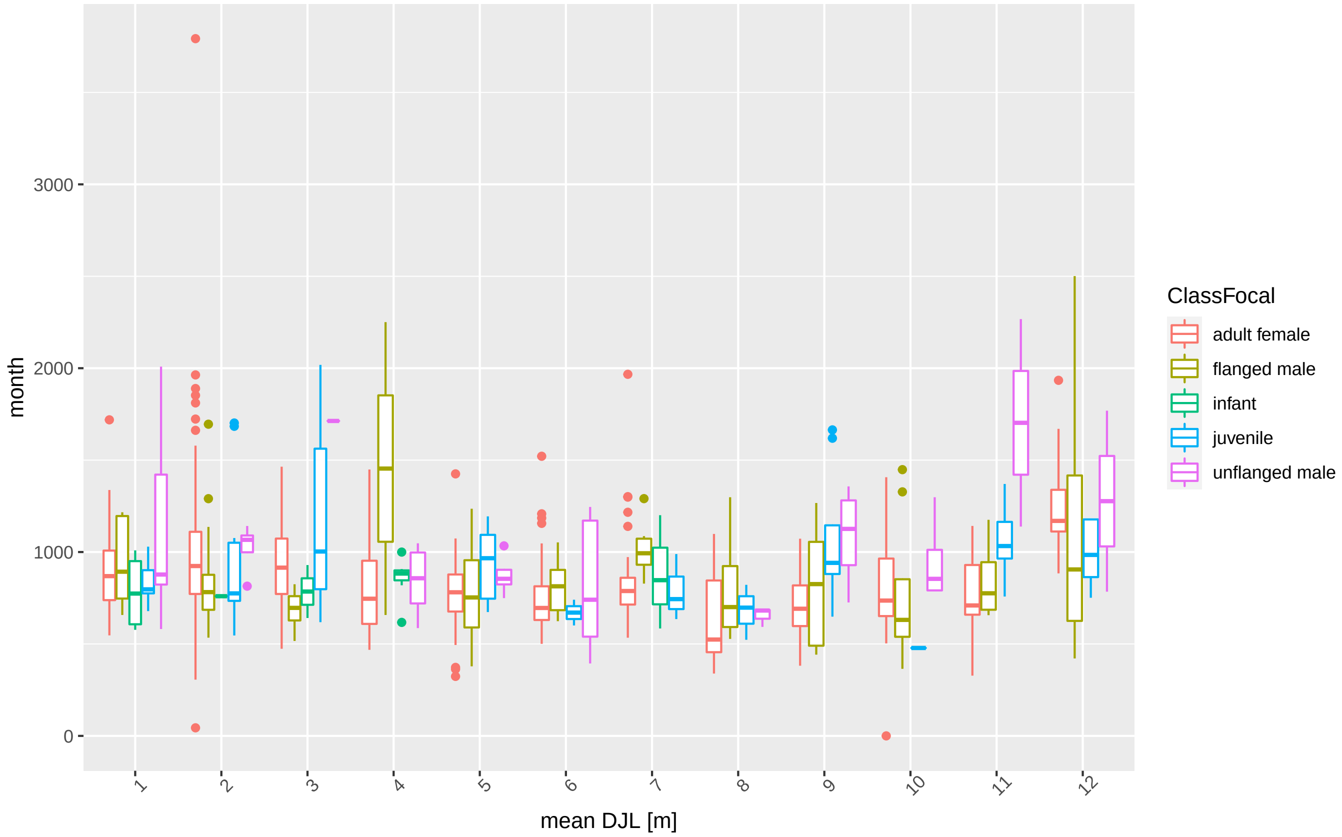
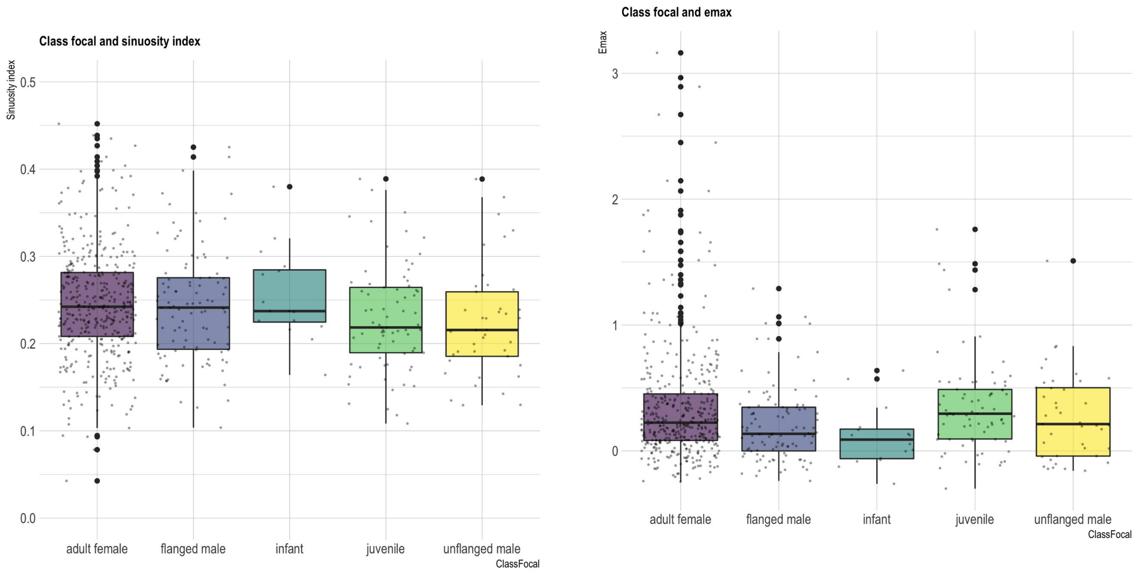
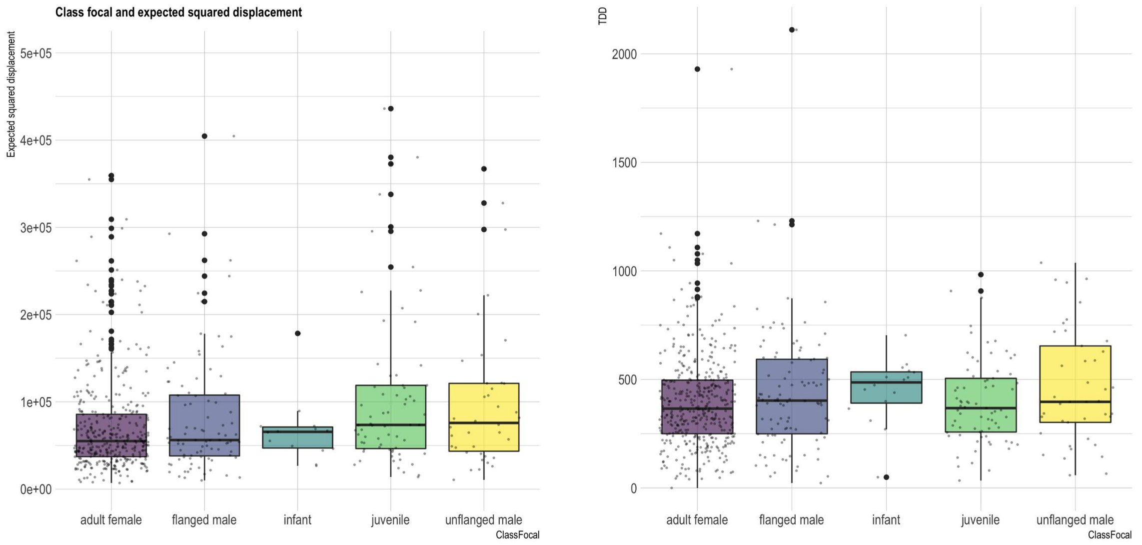


Figure B.11 – Day journey lengths over the year per age-sex class.



(a) sinuosity index (Benhamou, 2004)

(b) Maximum expected displacement, $E_{\max}$ (Cheung et al., 2007)



(c) Net squared displacement (Bunnefeld et al., 2011)

(d) total displacement

Figure B.12 – Derived tortuosity parameter for age-sex classes.

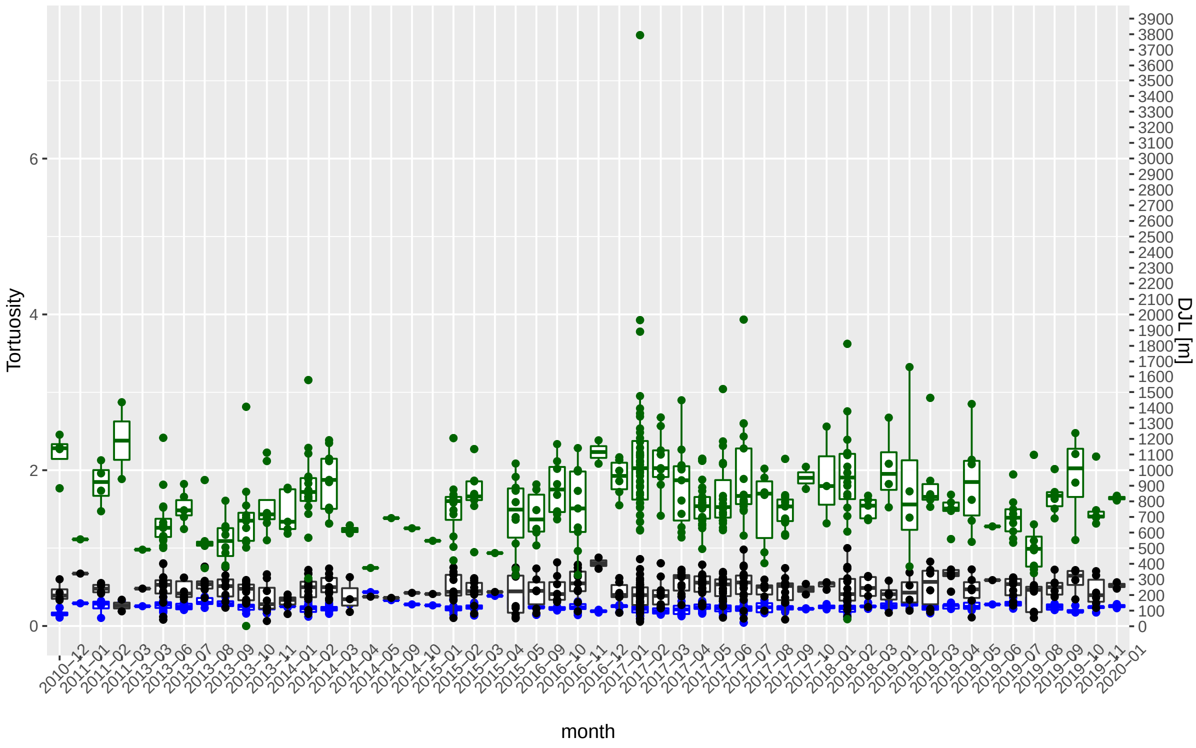


Figure B.13 – Overview of DJL (green), SI (black) and sinuosity index (blue) over the whole study period.

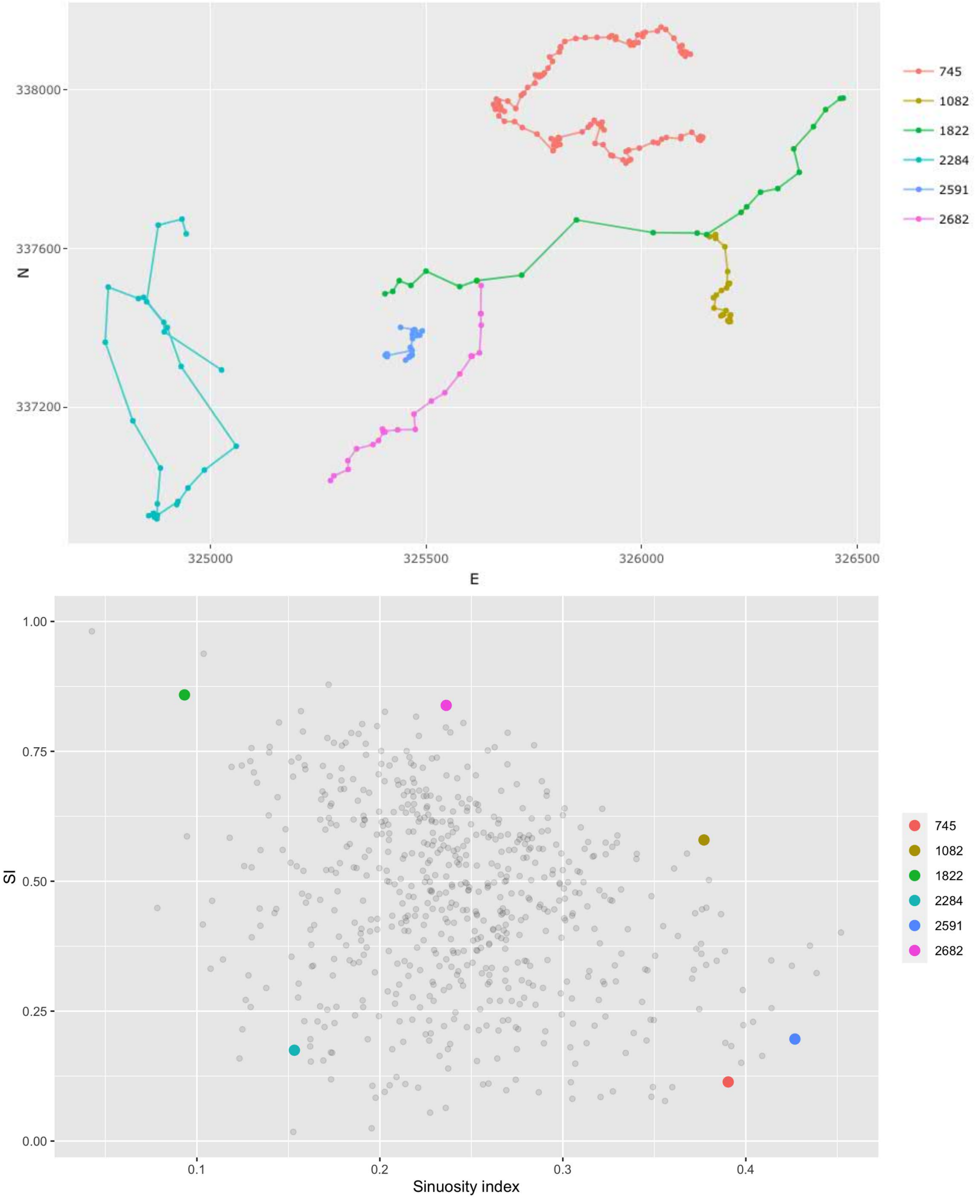
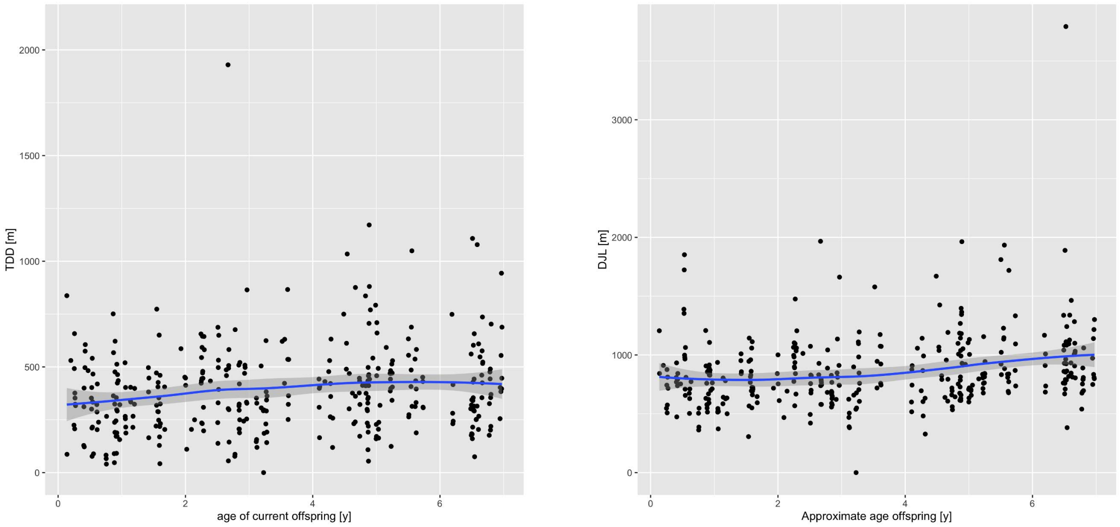


Figure B.14 – A selection of follows to compare the results of the sinuosity and the straightness. The follow 1822 has low sinuosity and high straightness, the follows 745, 2591 have low straightness and high sinuosity. These follows are as expected describing more or less tortuous movement which is reflected in both movement parameters. On the other hand shows the follow 1082 and the follow 2682 high sinuosity and also high straightness and the follow 2284 low sinuosity and low straightness. For these follows we get contradicting results when are interested in the tortuosity of movement.

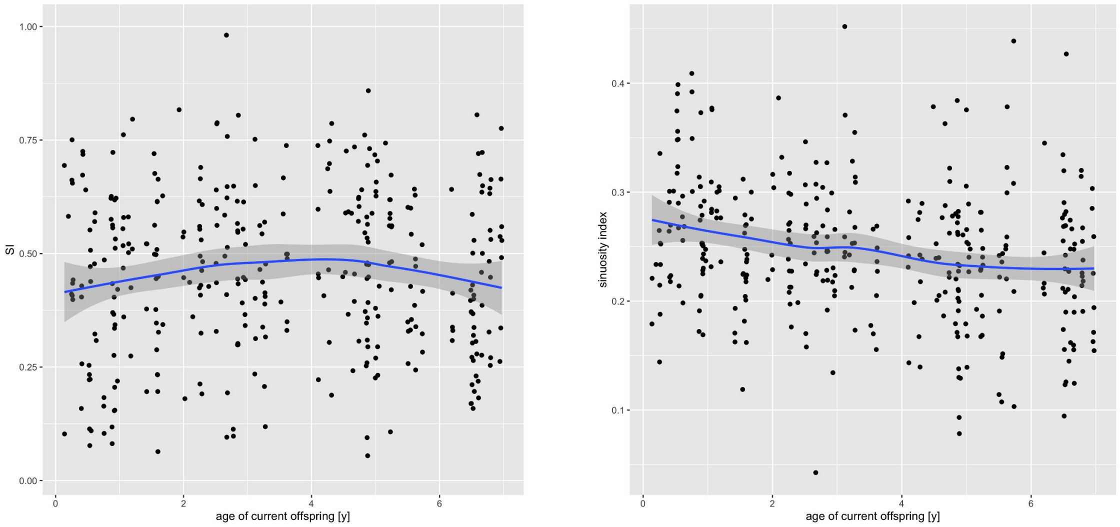
Table B.2 – Statistical models trying to explain TDD per follow for all age sex classes and for females with offspring only.

Nr.	**Response variable / Model description**	**Factor**	**Factor type**	**Estimate**	**Confidence Interval**	**P**	**VIF**
a)	Total displacement of all age sex classes	Intercept	intercept	114.24	-488.66 – 717.15	0.71	-
	n = 610	Day rain	Predictor	-0.09	-1.52 – 1.35	0.907	1.0
	p = 0.84	Night rain	Predictor	0.2	-0.43 – 0.83	0.536	1.0
	M-R^2 = 0.015	Average day temp.	Predictor	10.34	-12.40 – 33.08	0.373	1.0
	C-R^2 = 0.154	FAI	Predictor	-0.43	-8.77 – 7.91	0.92	1.0
	Family = Gaussian	ASC: Flanged male	Predictor	53.08	-35.57 – 141.74	0.241	1.3
		ASC: Infant	Predictor	56.13	-87.84 – 200.11	0.445	1.2
		ASC: Independant immature	Predictor	33.12	-55.06 – 121.30	0.462	1.3
		ASC: Unflanged male	Predictor	83.83	-19.90 – 187.56	0.113	1.2
		Focal	Random	-	-	**0.0047**	-
		Month Year	Random	-	-	0.23	-
b)	Total displacement of only females	Intercept	intercept	96.19	-709.29 – 901.68	0.815	-
	n = 340	Day rain	Predictor	-0.73	-2.35 – 0.89	0.375	1.0
	p = 0.14	Night rain	Predictor	-0.3	-1.27 – 0.67	0.541	1.0
	M-R2 = 0.030	Average day temp.	Predictor	10.03	-20.10 – 40.17	0.514	1.0
	C-R2 = 0.054	FAI	Predictor	-4.66	-14.48 – 5.16	0.352	1.0
	Family = Gaussian	Age of current offspring	Predictor	13.99	2.50 – 25.48	**0.017**	1.0
		Dominance category	Predictor	13.38	-21.35 – 48.12	0.45	1.0
		Focal	Random	-	-	0.46	-
		Month Year	Random	-	-	0.69	-

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; bold = significance level reached; Statistical variables info's see first table



(a) TDD and age of offspring **(b)** DJL and age of offspring



(c) SI and age of offspring **(d)** Sinuosity and age of offspring

Figure B.15 – DJL and TDD positively correlated with the age of the current offspring for females. But interestingly the TDD increased first around the age of 1 or 2 and DJL increased later around the age of 4. Therefore the straightness index shows a linear non-relationship because the relation follows a parable where the movement was straightest around the age of 3 to 4. But tortuosity measured witb the straightness index showed a decrease of sinuosity with age of the offspring.

B.2.3 Fruit trees visited

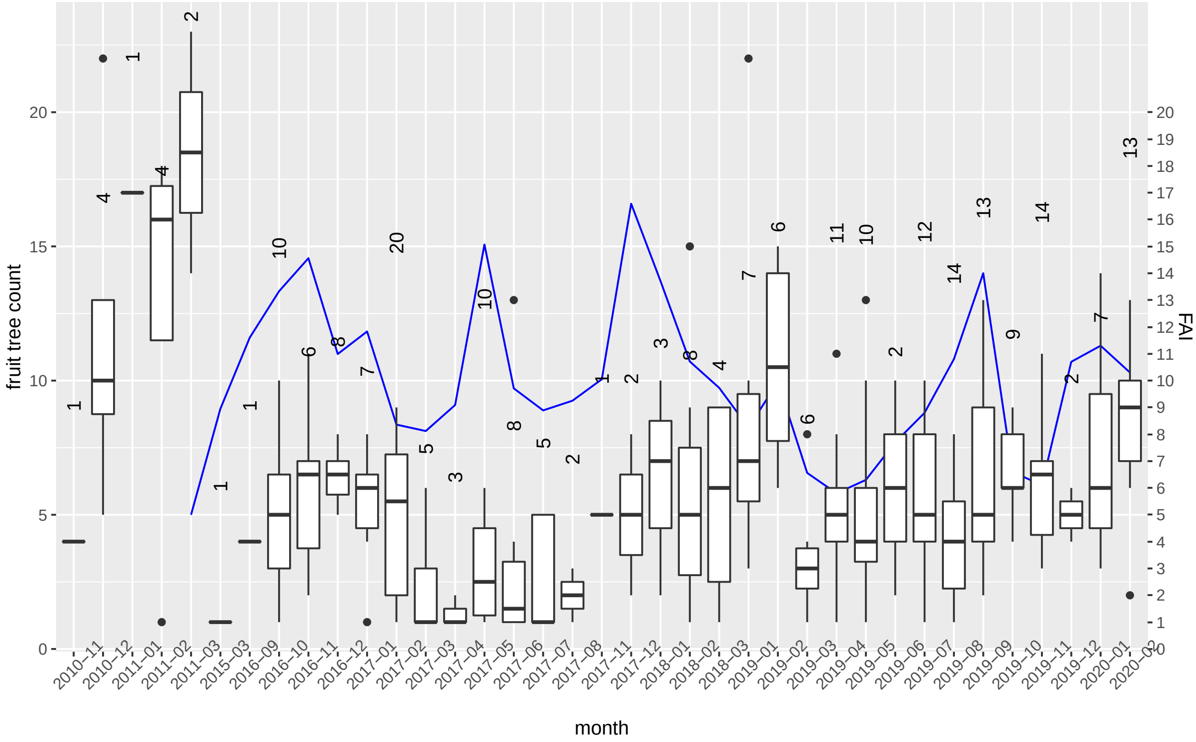


Figure B.16 – Comparison of fruit trees visited (boxplot) and monthly fruit availability index (blue line).

B.2.4 Differences of movement parameters and year-months

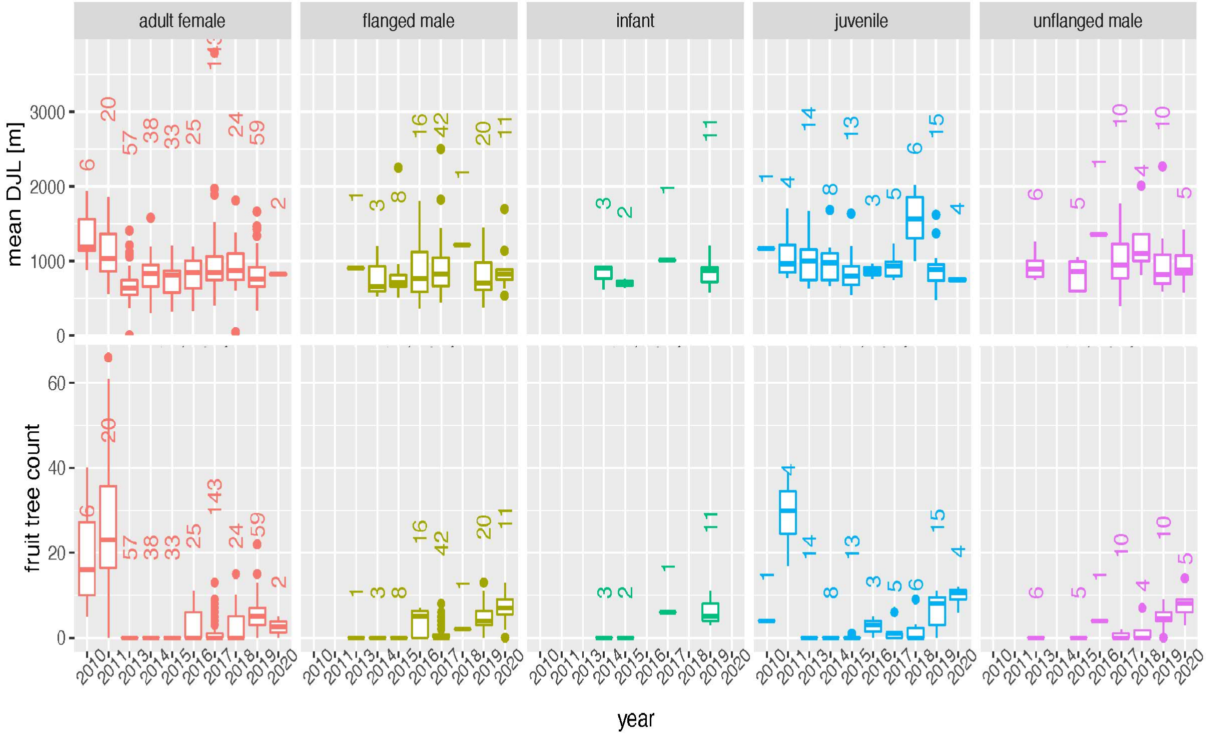


Figure B.17 – Differences of movement parameters between years.

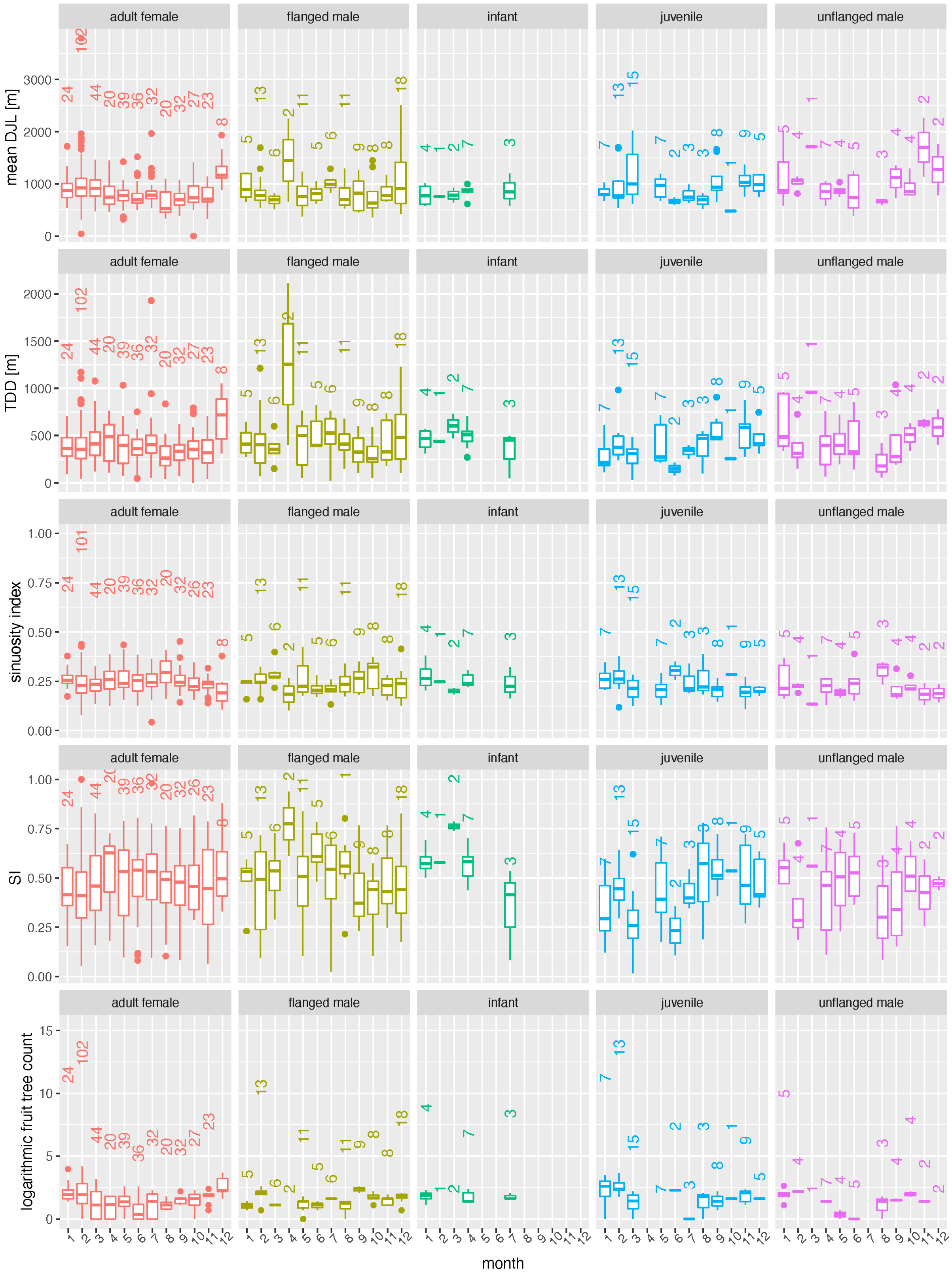


Figure B.18 – Differences of movement parameters between months.

B.2.5 Level 3: tortuosity and patterns during the day

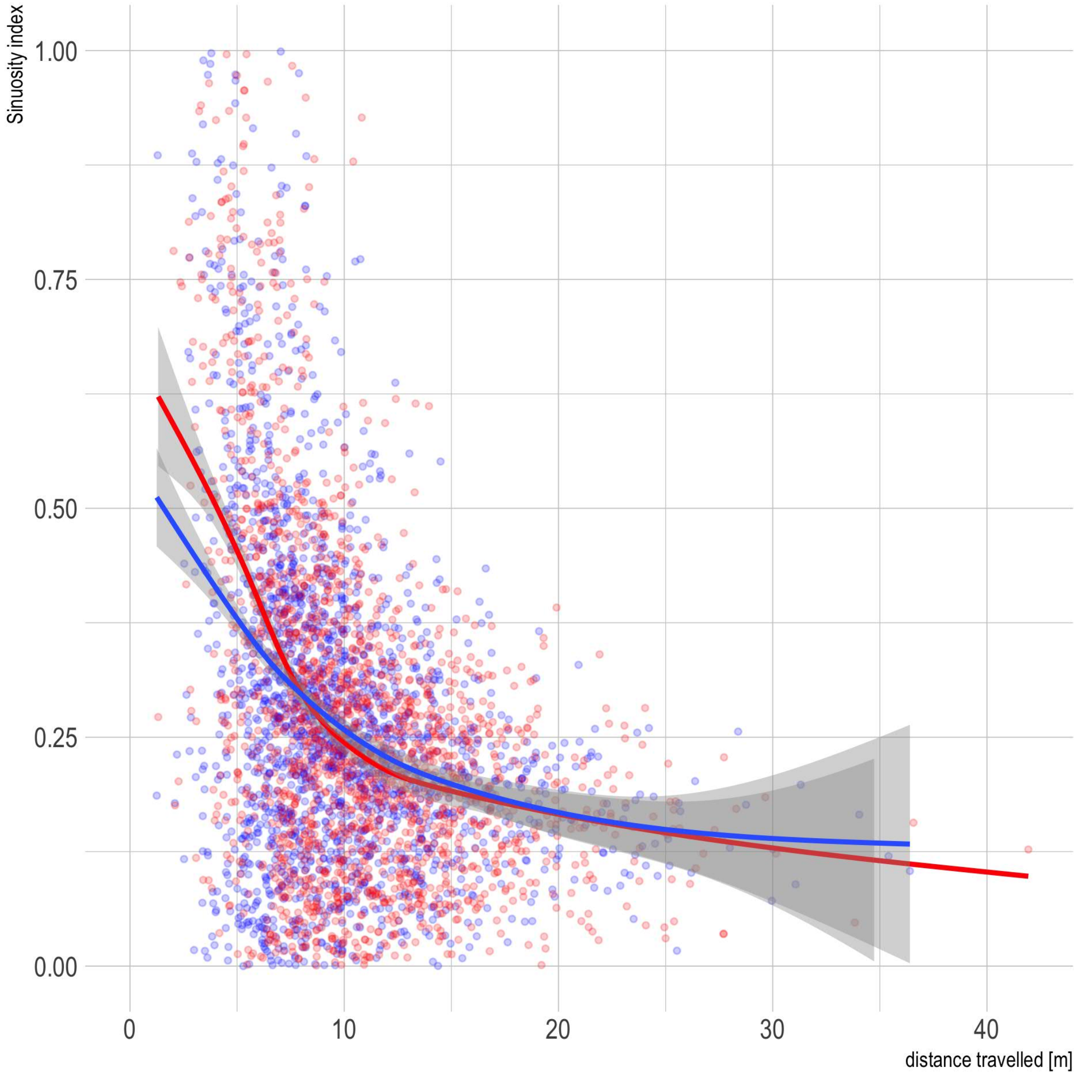


Figure B.19 – Comparison of tree to tree movement with a random sample with the same movement windows. In red is the random sample and in blue the tree to tree movement. The travel distance on the y axis was square root transformed for better visibility. Due to the randomness of the random sample the data was reproduced ten times but the results remained similar.

Table B.3 – Statistical models trying to explain sinuosity of movement between feeding trees.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	Sinuosity between trees	Intercept	intercept	-0.0085	-1.6817 – 1.6647	0.992	-
	n = 1501	Day rain	Predictor	-0.0022	-0.0093 – 0.0049	0.544	1.060559
	P =0.81	Night rain	Predictor	0	-0.0019 – 0.0019	0.989	1.045544
	M-R2 = 0.004	Average day temp.	Predictor	0.0188	-0.0463 – 0.0839	0.571	1.136826
	C-R2 = 0.0843	FAI	Predictor	-0.0139	-0.0318 – 0.0040	0.128	1.106368
	Family = Gaussian	ASC: Flanged male	Predictor	-0.0356	-0.1593 – 0.0881	0.573	1.202329
		ASC: Infant	Predictor	-0.0532	-0.2854 – 0.1789	0.653	1.077536
		ASC: Independant immature	Predictor	-0.072	-0.2171 – 0.0730	0.33	1.112555
		ASC: Unflanged male	Predictor	0.0091	-0.1381 – 0.1562	0.904	1.128103
		Date	Random	-	-	**0.0015**	-
		Focal	Random	-	-	0.8166	-
		N-fixes (between trees)	Random	-	-	**0.015**	-
		Time between trees	Random	-	-	0.99	-
b)	Sinuosity between trees	Intercept		-1.8082	-6.1276 – 2.5111	0.412	-
	n = 613	Day rain		-0.005	-0.0281 – 0.0181	0.672	1.056858
	P = 0.34	Night rain		-0.0002	-0.0048 – 0.0045	0.944	1.031573
	M-R2 = 0.016	Average day temp.		0.0961	-0.0641 – 0.2563	0.24	1.069871
	C-R2 = 0.090	FAI		-0.029	-0.0692 – 0.0111	0.156	1.036368
	Family = Gaussian	Dominance		-0.0798	-0.2236 – 0.0640	0.277	1.513861
		Age of current offspring		0.0149	-0.0468 – 0.0766	0.635	1.379508
		Matriline		0.0673	-0.1701 – 0.3047	0.579	1.163642
		Date	Random	-	-	**0.036**	-
		Focal	Random	-	-	0.999	-
		N-fixes (between trees)	Random	-	-	0.265	-
		Time between trees	Random	-	-	1	-

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; bold = significance level reached; Statistical variables info's see first table

Appendix C

Appendix: Home ranges

Table C.1 – Overview of adult and independent immature females used for the home range analysis.

Individual	ClassFocal	Birthdate	M	D	Follows	1. offspring	Birth date	2. offspring	Birth date	3. offspring	Birth date	Mother
cissy	adult female	01.01.65	1	2	74	Lisa	01.07.87	Chindy	01.01.03	Cinmon	01.04.12	-
sarabi	adult female	01.01.85	1	3	21	Sazu	01.01.07	Simba	01.03.13	-	-	-
lisa	adult female	01.07.87	1	3	162	Lilly	-	Lois	01.08.10	Leon	01.11.18	Cissy
lilly	adult female	01.03.01	1	4	42	Luther	01.03.16	-	-	-	-	Lisa
friska	adult female	01.01.43	2	1	166	Ellie	01.03.99	Fredy	01.06.05	Frankie	01.08.12	-
raffi	adult female	01.01.73	2	2	31	Ti	01.01.98	Rondaldo	01.01.06	Rendang	15.07.13	Halte
ellie	adult female	01.03.99	2	3	148	Eden	01.11.14	-	-	-	-	Friska
yulia	independent immature	01.01.07	2	4	45	-	-	-	-	-	-	-
tiara	adult female	-	3	-	11	-	-	-	-	-	-	-
trident	independent immature	01.07.06	3	4	32	-	-	-	-	-	-	Tiara

M = Matriline, D = Dominance

Table C.2 – Overview of derived bandwidths for different bandwidth estimators for the KDE algorithm

focal	hpi	hbcv	hscv
cissy	76.52	124.53	82.65
ellie	52.45	79.25	54.65
friska	53.74	87.07	55.93
lilly	72.33	116.48	76.77
lisa	56.79	89.73	60.83
raffi	70.31	127.59	74.12
sarabi	57.21	94.46	63.86
tiara	91.60	136.71	95.82
trident	70.28	97.94	77.68
yulia	50.43	83.21	53.23

Table C.3 – Overview of the results of the HR calculation for different HRE.

Orangutan							Core range 50%								Home range 95%							
focal	matriline	age cat.	dominance	nF	nGPS	Algo	area	n Tree	norm Tree	AUC	Compact.	Holes	nPoly	area holes	area	n Tree	norm Tree	AUC	Compact.	Holes	nPoly	area holes
friska	2	5	1	162	3807	akde	0.56	1109	0.118	*NA*	0.66	0	1	0	2.26	2614	0.11	*NA*	0.7	0	1	0
friska	2	5	1	162	3807	brb	0.52	1015	0.113	0.978	0.34	0	4	0	1.9	2411	0.113	0.978	0.33	0	3	0
friska	2	5	1	162	3807	kde	0.48	1063	0.118	0.981	0.27	0	5	0	1.75	2366	0.113	0.981	0.5	0	4	0
friska	2	5	1	162	3807	mcp	0.6	1097	0.116	*NA*	0.96	0	1	0	1.75	2260	0.111	*NA*	0.79	0	1	0
lisa	1	3	3	156	3881	akde	0.6	1151	0.125	*NA*	0.76	0	1	0	2.78	2768	0.113	*NA*	0.69	0	1	0
lisa	1	3	3	156	3881	brb	0.54	1272	0.13	0.975	0.52	0	1	685.12	2.31	2675	0.114	0.975	0.36	0	2	0
lisa	1	3	3	156	3881	kde	0.48	1115	0.132	0.976	0.42	0	2	0	2.03	2623	0.116	0.976	0.32	0	5	0
lisa	1	3	3	156	3881	mcp	0.49	1065	0.128	*NA*	0.97	0	1	0	2.32	2607	0.114	*NA*	0.82	0	1	0
ellie	2	2	3	138	3405	akde	0.45	972	0.112	*NA*	0.73	0	1	0	1.83	2449	0.111	*NA*	0.72	0	1	0
ellie	2	2	3	138	3405	brb	0.45	995	0.11	0.982	0.5	0	1	0	1.67	2176	0.109	0.982	0.65	0	1	0
ellie	2	2	3	138	3405	kde	0.4	1009	0.118	0.984	0.62	1	1	4067.34	1.57	2080	0.109	0.984	0.63	2	1	12602.96
ellie	2	2	3	138	3405	mcp	0.41	919	0.118	*NA*	0.95	0	1	0	1.6	2129	0.106	*NA*	0.9	0	1	0
cissy	1	4	2	74	1584	akde	0.94	1802	0.124	*NA*	0.54	0	1	0	3.55	2936	0.11	*NA*	0.7	0	1	0
cissy	1	4	2	74	1584	brb	0.7	1231	0.125	0.96	0.28	0	3	0	2.38	2683	0.113	0.96	0.48	1	2	6484.31
cissy	1	4	2	74	1584	kde	0.74	1343	0.126	0.958	0.3	0	1	0	2.49	2747	0.114	0.958	0.51	0	1	0
cissy	1	4	2	74	1584	mcp	0.92	1670	0.118	*NA*	0.9	0	1	0	2.5	2719	0.111	*NA*	0.82	0	1	0
yulia	2	1	4	43	872	akde	0.39	363	0.095	*NA*	0.64	0	1	0	1.55	1177	0.1	*NA*	0.66	0	1	0
yulia	2	1	4	43	872	brb	0.25	268	0.087	0.987	0.33	0	1	0	0.98	766	0.096	0.987	0.42	0	2	0
yulia	2	1	4	43	872	kde	0.23	253	0.086	0.989	0.28	0	2	0	0.9	671	0.092	0.989	0.31	0	3	0
yulia	2	1	4	43	872	mcp	0.28	322	0.099	*NA*	0.83	0	1	0	0.9	775	0.101	*NA*	0.67	0	1	0
lilly	1	2	4	39	805	akde	0.61	717	0.124	*NA*	0.57	0	1	0	2.4	2484	0.119	*NA*	0.57	0	1	0
lilly	1	2	4	39	805	brb	0.47	608	0.125	0.973	0.38	0	2	0	1.65	2057	0.124	0.973	0.35	0	3	0
lilly	1	2	4	39	805	kde	0.49	596	0.134	0.973	0.29	0	3	0	1.71	2056	0.124	0.973	0.36	0	2	0
lilly	1	2	4	39	805	mcp	0.55	761	0.129	*NA*	0.93	0	1	0	1.63	1955	0.126	*NA*	0.71	0	1	0
raffi	2	4	2	31	568	akde	0.85	959	0.103	*NA*	0.53	0	1	0	3.59	2671	0.109	*NA*	0.55	0	1	0
raffi	2	4	2	31	568	brb	0.38	407	0.096	0.977	0.15	0	2	0	1.69	1450	0.102	0.977	0.28	0	2	0
raffi	2	4	2	31	568	kde	0.38	407	0.098	0.975	0.15	0	3	0	1.75	1493	0.101	0.975	0.28	0	2	0
raffi	2	4	2	31	568	mcp	0.43	450	0.087	*NA*	0.68	0	1	0	1.95	1655	0.101	*NA*	0.54	0	1	0
trident	3	1	4	28	453	akde	0.36	322	0.087	*NA*	0.68	0	1	0	1.61	1394	0.106	*NA*	0.61	0	1	0
trident	3	1	4	28	453	brb	0.31	396	0.112	0.982	0.43	0	2	0	1.19	933	0.103	0.982	0.36	0	2	0
trident	3	1	4	28	453	kde	0.31	261	0.088	0.981	0.39	0	2	0	1.22	961	0.102	0.981	0.47	0	1	0
trident	3	1	4	28	453	mcp	0.32	250	0.086	*NA*	0.88	0	1	0	1.1	784	0.098	*NA*	0.65	0	1	0
sarabi	1	3	3	21	473	akde	0.63	955	0.106	*NA*	0.74	0	1	0	2.78	2495	0.11	*NA*	0.68	0	1	0
sarabi	1	3	3	21	473	brb	0.21	284	0.083	0.989	0.09	0	3	0	0.84	1012	0.105	0.989	0.27	0	2	0
sarabi	1	3	3	21	473	kde	0.21	306	0.09	0.989	0.09	0	4	0	0.83	992	0.107	0.989	0.26	0	2	0
sarabi	1	3	3	21	473	mcp	0.29	431	0.1	*NA*	0.76	0	1	0	0.8	828	0.102	*NA*	0.31	0	1	0
tiara	3	*NA*	*NA*	10	172	akde	0.6	906	0.097	*NA*	0.74	0	1	0	2.36	2522	0.109	*NA*	0.76	0	1	0
tiara	3	*NA*	*NA*	10	172	brb	0.3	394	0.091	0.988	0.15	0	5	0	1.03	1335	0.099	0.988	0.44	1	1	41086.16
tiara	3	*NA*	*NA*	10	172	kde	0.37	503	0.095	0.982	0.19	0	5	0	1.28	1704	0.105	0.982	0.5	0	1	0
tiara	3	*NA*	*NA*	10	172	mcp	0.43	715	0.095	*NA*	0.69	0	1	0	0.88	1280	0.102	*NA*	0.55	0	1	0

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; ***** model better than the null model

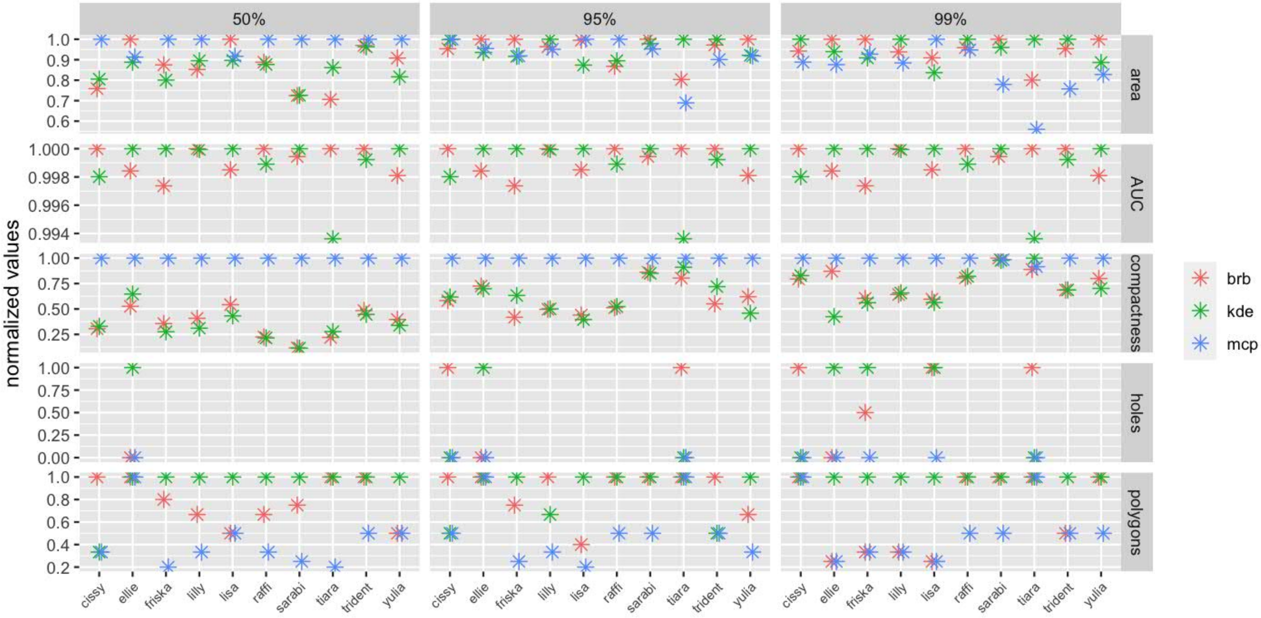


Figure C.1 – Home range descriptors of the three HRE algorithms KDE, BRB and MCP. The values are normalised per highest value of the category for better comparison.

C.0.1 Results home range

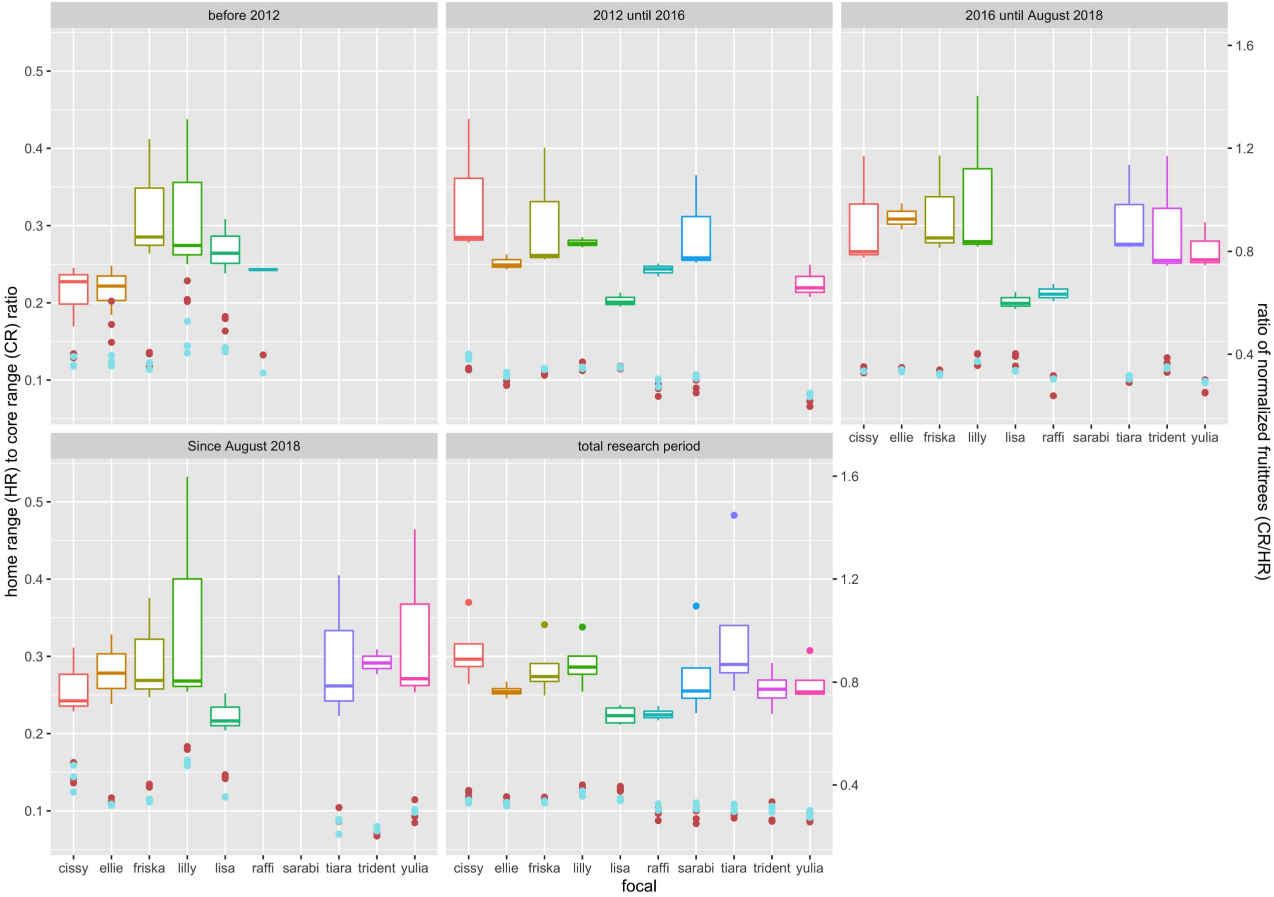
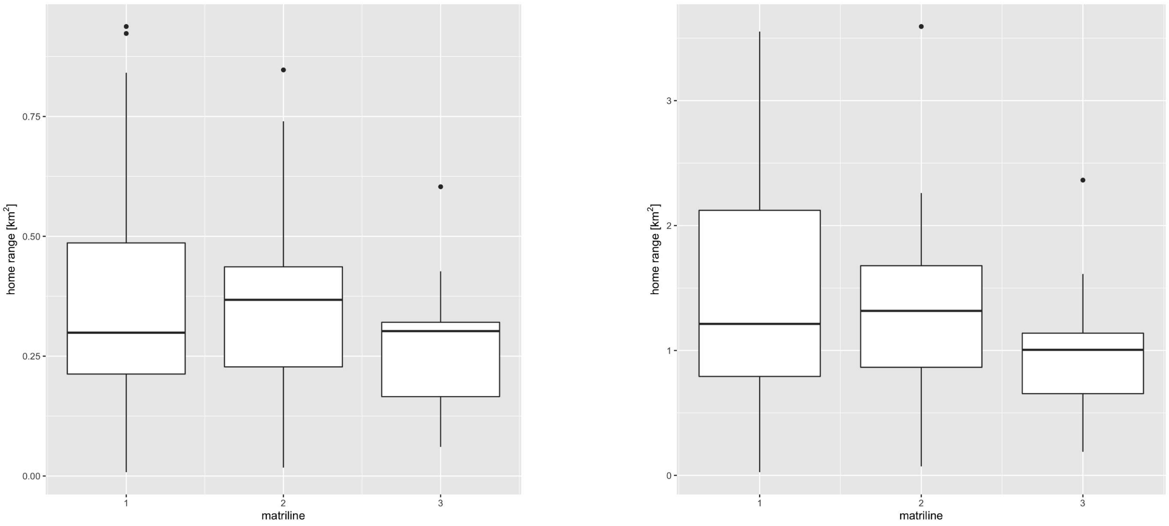


Figure C.2 – Results of ratio between core range and home ranges. Core ranges are on average 27±6% (average of all periods and HRE) of the 95% HR. Normalised fruit tree counts (divided by total sampling effort) were often more abundant in the core ranges (red dots) than in the full home ranges (blue dots).



(a) Core ranges **(b)** Home ranges

Figure C.3 – Home range size and matriline for core range and home range.

Table C.4 – Statistical models trying to explain normalized fruit trees values in overlaps and home ranges.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P
a)	Fruit trees in CR	Intercept	Intercept	0.1769	0.1302 – 0.2236	**<0.001**
	n = 121	Area	Predictor	-0.0559	-0.0755 – -0.0362	**<0.001**
	P <0.0001***	Matriline	Predictor	-0.0195	-0.0377 – -0.0013	**0.036**
	M-R2 = 0.25	Dominance	Predictor	-0.0038	-0.0160 – 0.0084	0.54
	C-R2 = 0.59	Focal	Random	-	-	**<0.001**
	Family = Gaussian	Algorithm	Random	-	-	**<0.001**
b)	Fruit trees in HR	Intercept	Intercept	0.1586	0.1329 – 0.1844	**<0.001**
	n = 190	Area	Predictor	-0.011	-0.0139 – -0.0081	**<0.001**
	P <0.0001***	Related	Predictor	-0.0137	-0.0235 – -0.0039	**0.006**
	M-R2 = 0.36	Dominance	Predictor	-0.003	-0.0096 – 0.0035	0.363
	C-R2 = 0.72	Focal	Random	-	-	**<0.001**
	Family = Gaussian	Algorithm	Random	-	-	0.13
c)	Fruit trees in overlaps of CR	Intercept	Intercept	0.0872	0.0710 – 0.1034	**<0.001**
	n = 164	Area	Predictor	0.0421	0.0148 – 0.0693	**0.002**
	P = 0.006**	Related	Predictor	-0.0036	-0.0141 – 0.0070	0.507
	M-R2 = 0.085	Dominance diff.	Predictor	0.0069	0.0008 – 0.0131	**0.027**
	C-R2 = 0.085	Focal	Random	-	-	1
	Family = Gaussian	Algorithm	Random	-	-	1
d)	Fruit trees in overlaps of HR	Intercept	Intercept	0.1105	0.1033 – 0.1176	**<0.001**
	n = 212	Area	Predictor	0.0003	-0.0032 – 0.0037	0.877
	P = 0.872	Related	Predictor	-0.0001	-0.0026 – 0.0025	0.96
	M-R2 = 0.0013	Dominance diff.	Predictor	0.0006	-0.0008 – 0.0021	0.406
	C-R2 = 0.162	Focal	Random	-	-	**<0.001**
	Family = Gaussian	Algorithm	Random	-	-	**0.042**

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; bold = significance level reached; Statistical variables info's see first table

C.0.2 Results overlaps

Table C.5 – Overview of Pearson's correlation coefficient between different overlap indices. The overlaps were calculated from the BRB home ranges for the whole study duration with a hmin factor of 0.8.

overlap	Jaccard index	BA index	UDOI	VI	relative HR shared
1.00	0.92	0.85	0.87	0.84	0.70
0.92	1.00	0.95	0.95	0.95	0.78
0.85	0.95	1.00	0.96	0.99	0.79
0.87	0.95	0.96	1.00	0.98	0.73
0.84	0.95	0.99	0.98	1.00	0.76
0.70	0.78	0.79	0.73	0.76	1.00

Table C.6 – Full ranging overlaps calculated from the UD (BA, UDOI, VI, relative HR shared) or the 95% delineation (overlap, Jaccard Index) of the BRB home ranges for the whole study duration with a hmin factor of 0.8.

focal	focal.1	related	overlap	algorithm	Jaccard index	BA index	UDOI	VI	relative HR shared
ellie	cissy	FALSE	1.70	brb	0.54	0.74	0.70	0.58	0.86
friska	cissy	FALSE	1.85	brb	0.53	0.73	0.70	0.58	0.74
lilly	cissy	TRUE	2.06	brb	0.64	0.80	0.79	0.61	0.85
lisa	cissy	TRUE	2.56	brb	0.74	0.87	1.02	0.69	0.80
raffi	cissy	FALSE	1.31	brb	0.38	0.50	0.30	0.32	0.67
sarabi	cissy	TRUE	0.63	brb	0.21	0.39	0.17	0.20	0.85
tiara	cissy	FALSE	0.93	brb	0.32	0.52	0.31	0.34	0.93
trident	cissy	FALSE	0.96	brb	0.27	0.41	0.19	0.23	0.60
yulia	cissy	FALSE	0.68	brb	0.19	0.36	0.16	0.24	0.50
cissy	ellie	FALSE	1.70	brb	0.54	0.74	0.70	0.58	0.60
friska	ellie	TRUE	1.87	brb	0.72	0.87	1.03	0.71	0.75
lilly	ellie	FALSE	1.58	brb	0.56	0.70	0.61	0.49	0.65
lisa	ellie	FALSE	1.67	brb	0.48	0.75	0.77	0.57	0.52
raffi	ellie	TRUE	0.92	brb	0.30	0.42	0.20	0.26	0.47
sarabi	ellie	FALSE	0.42	brb	0.18	0.40	0.20	0.24	0.57
tiara	ellie	FALSE	0.80	brb	0.37	0.55	0.36	0.39	0.80
trident	ellie	FALSE	0.50	brb	0.16	0.27	0.09	0.17	0.31
yulia	ellie	TRUE	0.91	brb	0.38	0.49	0.28	0.30	0.68
cissy	friska	FALSE	1.85	brb	0.53	0.73	0.70	0.58	0.65
ellie	friska	TRUE	1.87	brb	0.72	0.87	1.03	0.71	0.95
lilly	friska	FALSE	1.82	brb	0.58	0.71	0.63	0.49	0.75
lisa	friska	FALSE	1.84	brb	0.48	0.72	0.68	0.50	0.58
raffi	friska	TRUE	0.98	brb	0.28	0.37	0.15	0.21	0.50
sarabi	friska	FALSE	0.46	brb	0.16	0.28	0.10	0.13	0.62
tiara	friska	FALSE	0.81	brb	0.30	0.50	0.30	0.36	0.81
trident	friska	FALSE	0.55	brb	0.15	0.21	0.05	0.12	0.34
yulia	friska	TRUE	1.19	brb	0.44	0.65	0.54	0.44	0.88
cissy	lilly	TRUE	2.06	brb	0.64	0.80	0.79	0.61	0.72
ellie	lilly	FALSE	1.58	brb	0.56	0.70	0.61	0.49	0.79
friska	lilly	FALSE	1.82	brb	0.58	0.71	0.63	0.49	0.72
lisa	lilly	TRUE	2.08	brb	0.59	0.77	0.81	0.56	0.65
raffi	lilly	FALSE	0.79	brb	0.22	0.23	0.06	0.14	0.40
sarabi	lilly	TRUE	0.37	brb	0.13	0.19	0.04	0.08	0.49
tiara	lilly	FALSE	0.63	brb	0.22	0.29	0.09	0.18	0.62
trident	lilly	FALSE	0.45	brb	0.12	0.19	0.04	0.11	0.27
yulia	lilly	FALSE	0.74	brb	0.24	0.28	0.09	0.14	0.54
cissy	lisa	TRUE	2.56	brb	0.74	0.87	1.02	0.69	0.90
ellie	lisa	FALSE	1.67	brb	0.48	0.75	0.77	0.57	0.84
friska	lisa	FALSE	1.84	brb	0.48	0.72	0.68	0.50	0.73
lilly	lisa	TRUE	2.08	brb	0.59	0.77	0.81	0.56	0.86
raffi	lisa	FALSE	1.61	brb	0.46	0.60	0.53	0.39	0.82
sarabi	lisa	TRUE	0.70	brb	0.22	0.51	0.33	0.31	0.95
tiara	lisa	FALSE	0.96	brb	0.30	0.56	0.37	0.36	0.95
trident	lisa	FALSE	1.28	brb	0.36	0.57	0.48	0.36	0.80
yulia	lisa	FALSE	0.73	brb	0.19	0.25	0.07	0.13	0.54
cissy	raffi	FALSE	1.31	brb	0.38	0.50	0.30	0.32	0.46
ellie	raffi	TRUE	0.92	brb	0.30	0.42	0.20	0.26	0.46
friska	raffi	TRUE	0.98	brb	0.28	0.37	0.15	0.21	0.39
lilly	raffi	FALSE	0.79	brb	0.22	0.23	0.06	0.14	0.32
lisa	raffi	FALSE	1.61	brb	0.46	0.60	0.53	0.39	0.50
sarabi	raffi	FALSE	0.66	brb	0.32	0.62	0.47	0.43	0.89
tiara	raffi	FALSE	0.81	brb	0.38	0.59	0.48	0.43	0.81
trident	raffi	FALSE	1.08	brb	0.43	0.72	0.73	0.57	0.67
yulia	raffi	TRUE	0.60	brb	0.22	0.24	0.06	0.15	0.44
cissy	sarabi	TRUE	0.63	brb	0.21	0.39	0.17	0.20	0.22
ellie	sarabi	FALSE	0.42	brb	0.18	0.40	0.20	0.24	0.21
friska	sarabi	FALSE	0.46	brb	0.16	0.28	0.10	0.13	0.18
lilly	sarabi	TRUE	0.37	brb	0.13	0.19	0.04	0.08	0.15
lisa	sarabi	TRUE	0.70	brb	0.22	0.51	0.33	0.31	0.22
raffi	sarabi	FALSE	0.66	brb	0.32	0.62	0.47	0.43	0.33
tiara	sarabi	FALSE	0.37	brb	0.27	0.46	0.28	0.34	0.37
trident	sarabi	FALSE	0.67	brb	0.40	0.64	0.52	0.46	0.42
yulia	sarabi	FALSE	0.07	brb	0.03	0.04	0.00	0.02	0.05
cissy	tiara	FALSE	0.93	brb	0.32	0.52	0.31	0.34	0.33
ellie	tiara	FALSE	0.80	brb	0.37	0.55	0.36	0.39	0.40
friska	tiara	FALSE	0.81	brb	0.30	0.50	0.30	0.36	0.32
lilly	tiara	FALSE	0.63	brb	0.22	0.29	0.09	0.18	0.25
lisa	tiara	FALSE	0.96	brb	0.30	0.56	0.37	0.36	0.30
raffi	tiara	FALSE	0.81	brb	0.38	0.59	0.48	0.43	0.41
sarabi	tiara	FALSE	0.37	brb	0.27	0.46	0.28	0.34	0.51
trident	tiara	TRUE	0.41	brb	0.18	0.39	0.20	0.30	0.25
yulia	tiara	FALSE	0.44	brb	0.23	0.32	0.13	0.23	0.32
cissy	trident	FALSE	0.96	brb	0.27	0.41	0.19	0.23	0.34
ellie	trident	FALSE	0.50	brb	0.16	0.27	0.09	0.17	0.25
friska	trident	FALSE	0.55	brb	0.15	0.21	0.05	0.12	0.22
lilly	trident	FALSE	0.45	brb	0.12	0.19	0.04	0.11	0.18
lisa	trident	FALSE	1.28	brb	0.36	0.57	0.48	0.36	0.40
raffi	trident	FALSE	1.08	brb	0.43	0.72	0.73	0.57	0.55
sarabi	trident	FALSE	0.67	brb	0.40	0.64	0.52	0.46	0.91
tiara	trident	TRUE	0.41	brb	0.18	0.39	0.20	0.30	0.41
yulia	trident	FALSE	0.00	brb	0.00	0.00	0.00	0.00	0.00
cissy	yulia	FALSE	0.68	brb	0.19	0.36	0.16	0.24	0.24
ellie	yulia	TRUE	0.91	brb	0.38	0.49	0.28	0.30	0.46
friska	yulia	TRUE	1.19	brb	0.44	0.65	0.54	0.44	0.47
lilly	yulia	FALSE	0.74	brb	0.24	0.28	0.09	0.14	0.30
lisa	yulia	FALSE	0.73	brb	0.19	0.25	0.07	0.13	0.23
raffi	yulia	TRUE	0.60	brb	0.22	0.24	0.06	0.15	0.30
sarabi	yulia	FALSE	0.07	brb	0.03	0.04	0.00	0.02	0.09
tiara	yulia	FALSE	0.44	brb	0.23	0.32	0.13	0.23	0.43
trident	yulia	FALSE	0.00	brb	0.00	0.00	0.00	0.00	0.00

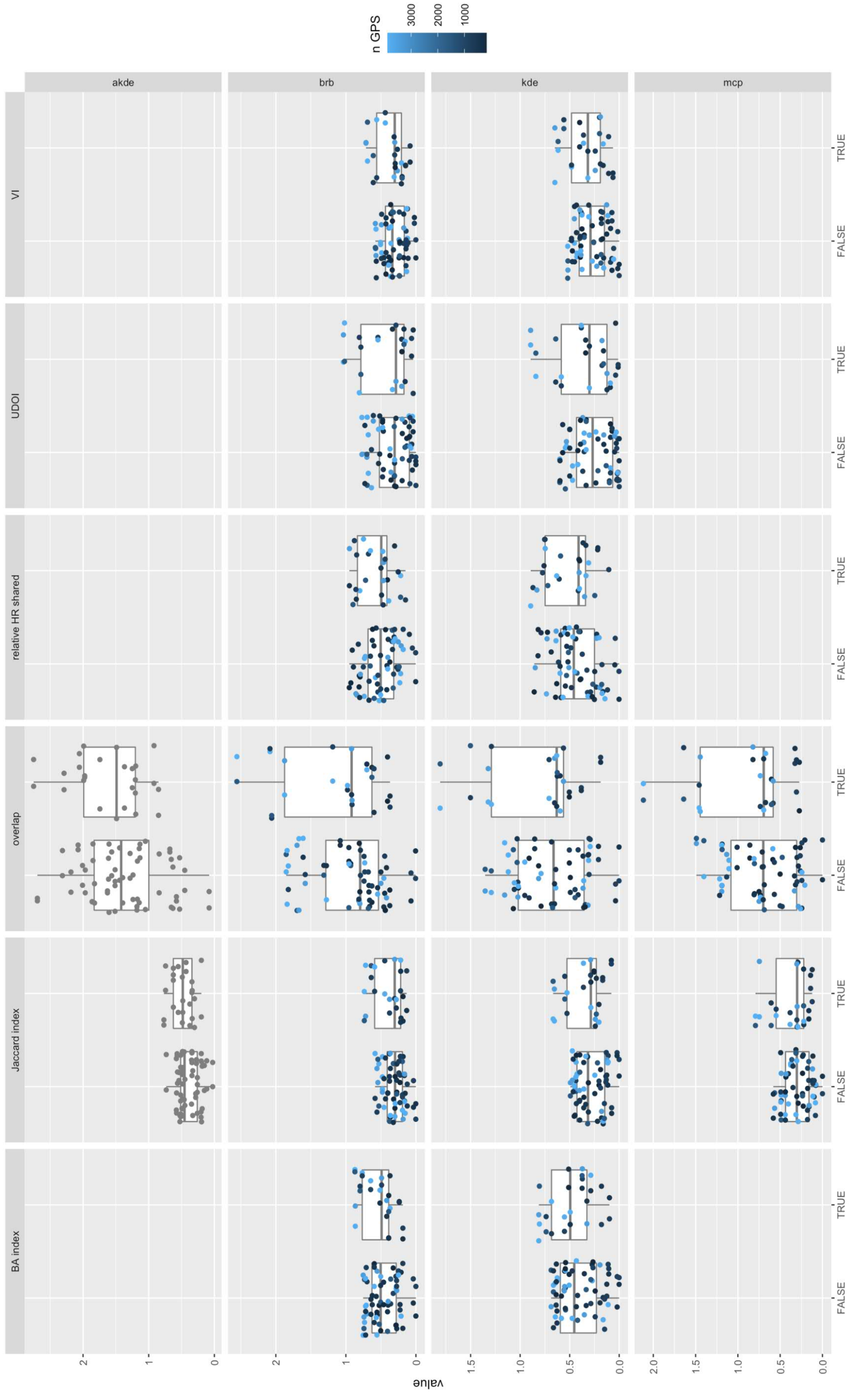


Figure C.4 – Difference of overlap indices for related and unrelated individuals for the full home ranges.

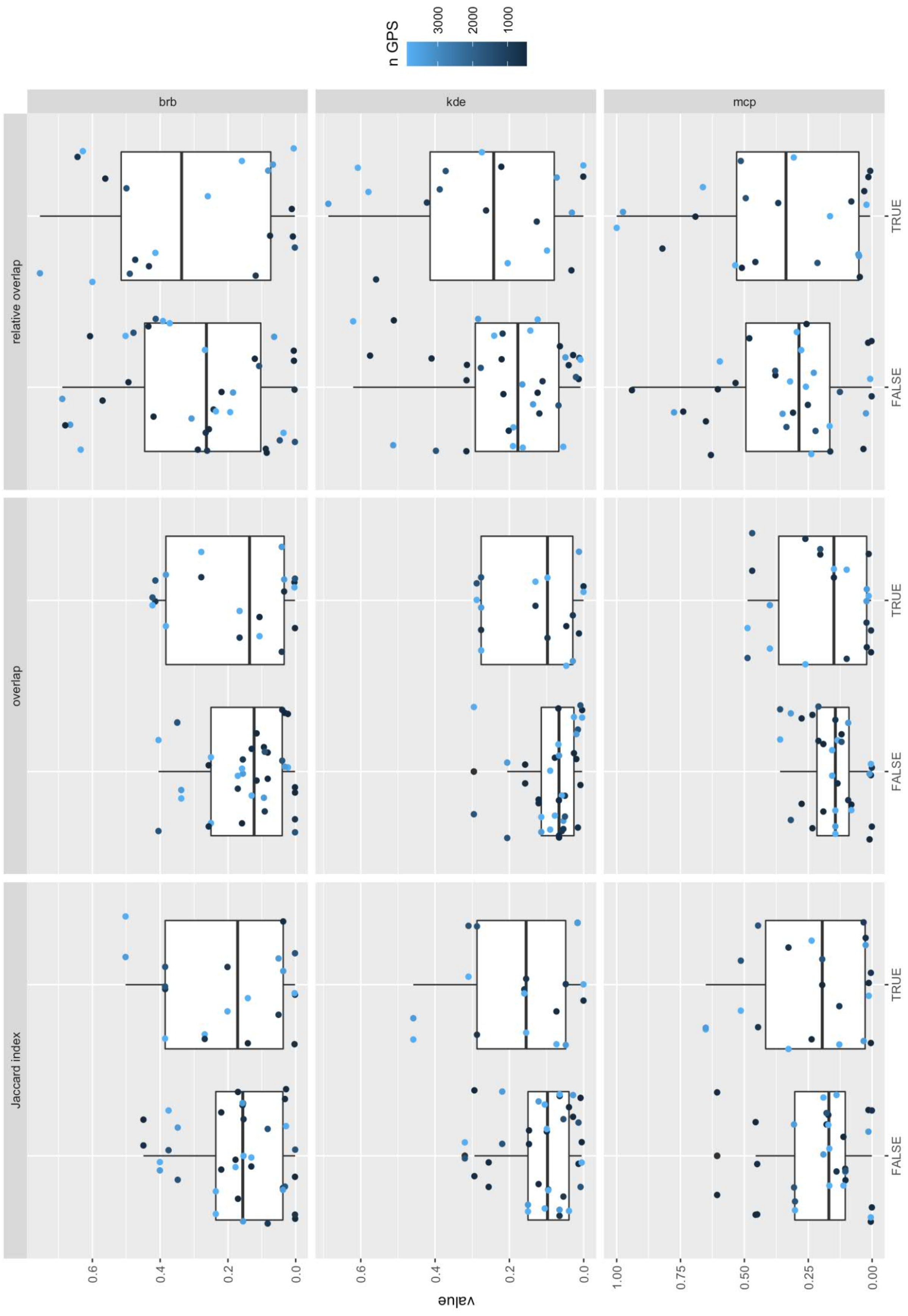


Figure C.5 – Difference of overlap indices for related and unrelated individuals.

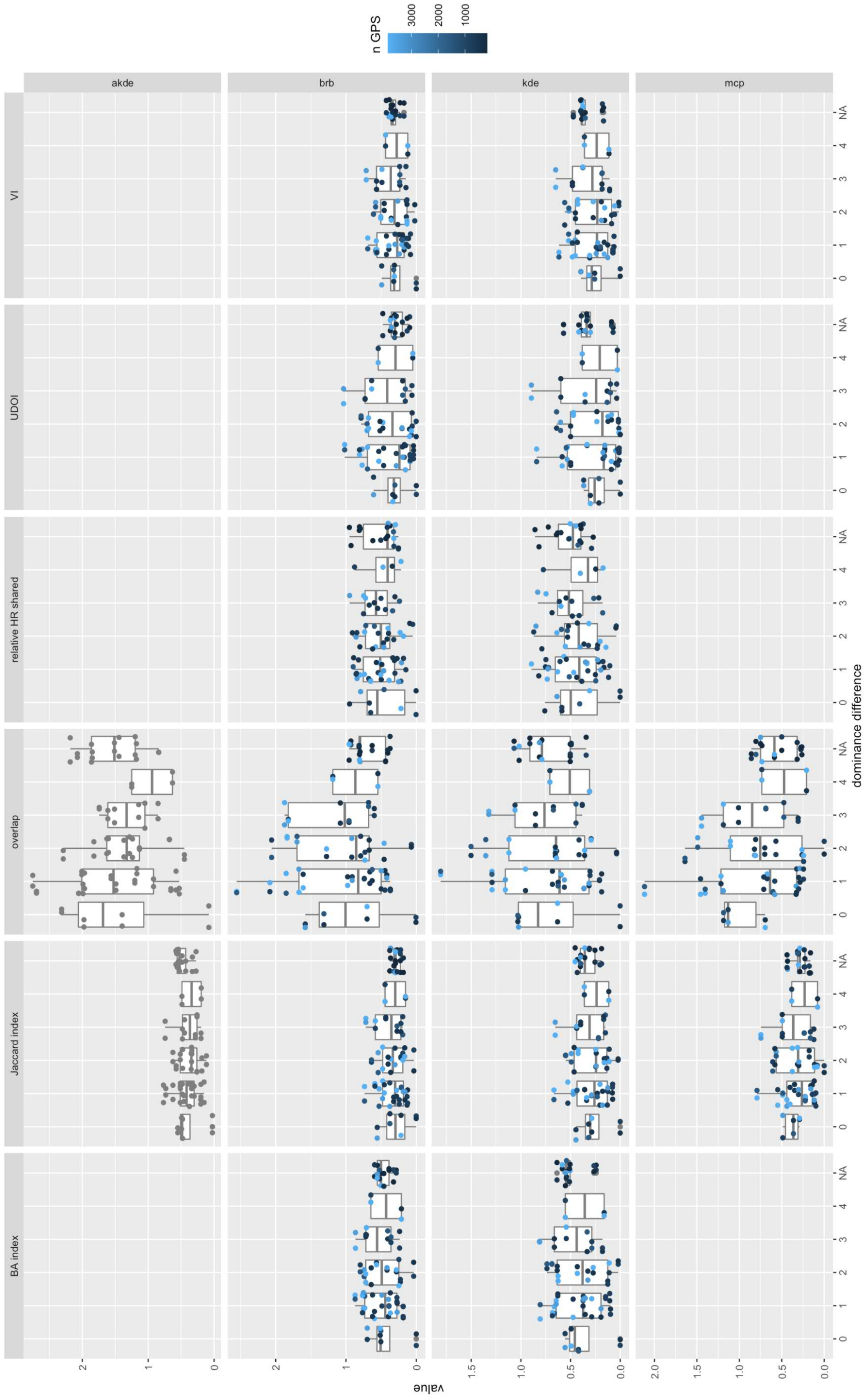
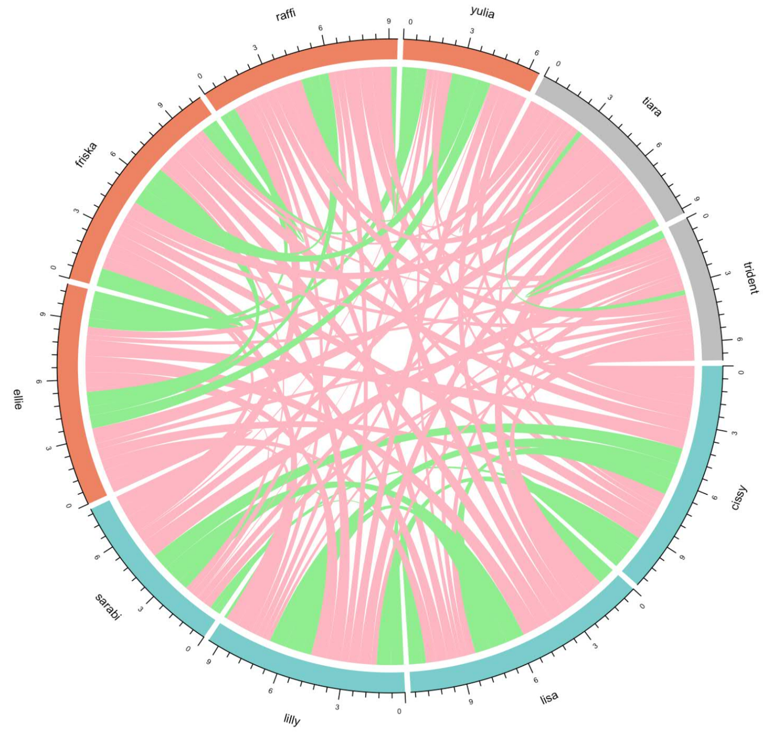
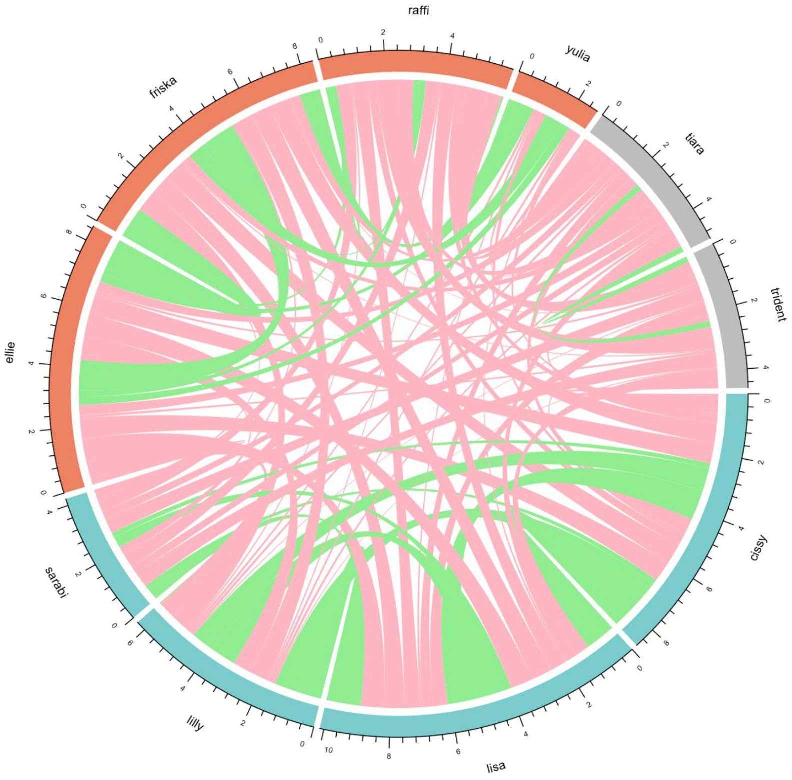


Figure C.6 – Difference of overlap indices for different dominance differences.



(a) area shared relative to HR



(b) UDOI

Figure C.7 – Overview of overlaps between individuals over total research period. Overlaps were derived from the BRB algorithm with a h_{min} scaling factor of 0.8. Overlaps shared with related individuals are indicated with green and overlaps shared with unrelated individuals are marked in red. The matrilines are marked in orange, blue and grey. The UDOI and the relative HR shared were calculated from the UD and not from the polygons.

Table C.7 – Statistical models trying to explain normalized fruit trees values in overlaps and home ranges.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P
a)	Fruit trees in CR	Intercept	Intercept	0.1769	0.1302 – 0.2236	**<0.001**
	n = 121	Area	Predictor	-0.0559	-0.0755 – -0.0362	**<0.001**
	P <0.0001* **	Matriline	Predictor	-0.0195	-0.0377 – -0.0013	**0.036**
	M-R2 = 0.25	Dominance	Predictor	-0.0038	-0.0160 – 0.0084	0.54
	C-R2 = 0.59	Focal	Random	-	-	**<0.001**
	Family = Gaussian	Algorithm	Random	-	-	**<0.001**
b)	Fruit trees in HR	Intercept	Intercept	0.1586	0.1329 – 0.1844	**<0.001**
	n = 190	Area	Predictor	-0.011	-0.0139 – -0.0081	**<0.001**
	P <0.0001* **	Related	Predictor	-0.0137	-0.0235 – -0.0039	**0.006**
	M-R2 = 0.36	Dominance	Predictor	-0.003	-0.0096 – 0.0035	0.363
	C-R2 = 0.72	Focal	Random	-	-	**<0.001**
	Family = Gaussian	Algorithm	Random	-	-	0.13
c)	Fruit trees in overlaps of CR	Intercept	Intercept	0.0872	0.0710 – 0.1034	**<0.001**
	n = 164	Area	Predictor	0.0421	0.0148 – 0.0693	**0.002**
	P = 0.006 **	Related	Predictor	-0.0036	-0.0141 – 0.0070	0.507
	M-R2 = 0.085	Dominance diff.	Predictor	0.0069	0.0008 – 0.0131	**0.027**
	C-R2 = 0.085	Focal	Random	-	-	1
	Family = Gaussian	Algorithm	Random	-	-	1
d)	Fruit trees in overlaps of HR	Intercept	Intercept	0.1105	0.1033 – 0.1176	**<0.001**
	n = 212	Area	Predictor	0.0003	-0.0032 – 0.0037	0.877
	P = 0.872	Related	Predictor	-0.0001	-0.0026 – 0.0025	0.96
	M-R2 = 0.0013	Dominance diff.	Predictor	0.0006	-0.0008 – 0.0021	0.406
	C-R2 = 0.162	Focal	Random	-	-	**<0.001**
	Family = Gaussian	Algorithm	Random	-	-	**0.042**

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; bold = significance level reached; Statistical variables info's see first table

Personal Declaration

Personal declaration: I hereby declare that the submitted thesis is the result of my own, independent work. All external sources are explicitly acknowledged in the thesis.

31.7.2021
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Place, Date Signature of author