Impact of Food Availability on Ranging Behaviour of the Sumatran Orangutans (Pongo abelii) at the Suaq Balimbing Population

GEO 511 Master's Thesis

Author
Tobias Riegger
07-156-227

Supervised by
Prof. Dr. Robert Weibel
Dr. Caroline Schuppli (cschuppli@ab.mpg.de)

Faculty representative
Prof. Dr. Robert Weibel

31.08.2022
Department of Geography, University of Zurich

Contact

Tobias Riegger
Röntgenstrasse 70
8005 Zürich
tobiasriegger@gmx.ch

Dr. Caroline Schuppli
Max Planck Institute of Animal Behavior
Development and Evolution of Cognition
Bücklestrasse 5a
78467 Konstanz
Germany

Prof. Dr. Robert Weibel
University of Zurich Department of Geography
Winterthurerstrasse 190
8057 Zurich

Abstract

Tobias RIEGGER

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Orangutans are the largest arboreal mammals on Earth, one of human's closest relatives, and a keystone species for biodiversity conservation, but they are threatened by extinction. Factors such as slow life history, large body size, frugivory, arboreal lifestyle, and low population density make them particularly vulnerable to population decline, especially when they face fragmentation and loss of habitat and wildlife trade. Therefore, scientists and conservationists alike are interested in their spatial and temporal ranging behavior and their ecological needs. Since they face different food availability in different tropical forests, orangutans likely adopt different strategies to ensure sufficient energy intake. Sumatran orangutans (*Pongo abelii*) in Suaq Balimbing spend most of their day searching for fruit. Further, they live in a habitat with higher fruit availability, in higher densities, and are more sociable than orangutans at other research sites. However, past studies found very little to no evidence that habitat fruit availability, represented as the percentage of fruit-bearing trees, has an effect on their ranging behavior. In contrast, several studies showed that the fluctuation of fruit availability in Bornean rain forests impacted the orangutans' range behavior in Tuanan on Borneo.

In the first part, this thesis aims to find an alternative way to represent food availability by looking at the actual feeding behavior of orangutans. I introduced a new food availability index called 'experienced FAI' (eFAI) and two sub-indices, which are based on this eFAI but split into a fruit (fruit eFAI) and non-fruit component (non-fruit eFAI). I analyzed and compared *behavioral and GPS data* from 2007 to 2021, collected in 1743 focal follow days and in accordance with standardized field methods by the Department of Anthropology of the University of Zurich and the Development and Evolution of Cognition Research Group at the Max Planck Institute of Animal Behavior in Konstanz, Germany. The eFAI was calculated based on a ratio of GPS points taken at fixed intervals throughout the focal follow to GPS points taken whenever the focal individual was feeding. I divided orangutans into four age-sex classes: adult females, flanged males, unflanged males, and independent immatures.

The results show that the comparison of *behavioral and GPS data* was needed to validate the accuracy of GPS points, complement feeding locations, and improve the eFAI calculation. A bootstrapping analysis revealed a minimum number of 10 follows per month to be an appropriate threshold. Regarding the traditional, habitat-centered fruit availability (termed hFAI in this study), I confirmed that Sumatran orangutans at Suaq do not face fruit scarcity throughout the year. Nevertheless, experienced food availability (eFAI) varied depending on the age-sex classes. Results suggest that flanged males spend extended time exploiting one resource rather than switching between resources. Independent immatures are most likely less competent at locating big food patches, and thus they end up switching between food patches faster than other individuals. However, I noticed that orangutans of different age-sex classes have similar diet compositions, except for adult females that showed broader diets, which may relate to maintaining lactation and pregnancy by consuming nutrient- and protein-rich food. The spatial and temporal analysis of the eFAI suggests that fruit availability patterns may be associated with the layout of the research site and vary between forest types. In contrast, non-fruit food items can be found everywhere.

In the second part, I investigated the effect of food availability on socio-spatial movement patterns. Therefore, I derived the Day Journey Length (DJL), Total Displacement Distance (TDD), and two tortuosity indices, the Straightness Index (SI) and the sinuosity index for the different age-sex classes and individuals. Fruit eFAI and non-fruit eFAI showed contradicting effects on the DJLs of orangutans and highlighted that an overall eFAI can explain less variation in ranging behavior. Fruit availability in the habitat (hFAI) could not explain any variation in the movement of orangutans, as expected based on the findings of previous studies, most likely because of the high abundance of fruit in Suaq. In contrast, I detected significant effects of fruit eFAI and non-fruit eFAI on DJL and sinuosity of movement but not on TDD and SI.

When flanged males increased their non-fruit consumption, they had shorter DJL. Shorter distances may relate to longer feeding times at their feeding locations. Further results suggest that adult females move the shortest distances but the most tortuous. Moving after independently moving but still dependent offspring or carrying their young offspring may lead to higher sinuosity and slow adult females down. Furthermore, adult females traveled longer and straighter distances when consuming more fruit but shorter distances when focusing on non-fruit food items. This behavior suggests that adult females know the locations of the fruit trees and how to get to them when fruit are available. However, on a focal level, I found that older females tend to stay put when more non-fruit food items are available, and younger females tend to travel more, suggesting they actively search for those items. Results for unflanged males and independent immatures suggest that the ranging behavior of both age-sex classes is not influenced by food availability. For unflanged males, the mating strategy may have a greater effect on their ranging behavior than food availability. In contrast, for independent immatures, social factors most likely play a more prominent role as they are more gregarious and social than adult orangutans.

In conclusion, comparing and complementing data sets and establishing new ways of representing food availability for Suaq proved to be meaningful, as I discovered different significant effects of experienced food availability on the movement parameters of Sumatran orangutans. However, differentiating between the availability of different food types is essential when looking at the effects of food availability on ranging. I suggest testing the approach in this thesis further at other research sites, which may help to understand the ranging behavior of orangutans better and protect them.

Acknowledgements

Special thanks go to my advisor Dr. Caroline Schuppli from the Development and Evolution of Cognition Research Group at the Max Planck Institute of Animal Behavior in Konstanz, Germany. She always had an open ear for my questions, sparked my interest in orangutans, and gave me advice and valuable feedback in no time. I highly appreciated her in-depth knowledge of orangutan behavior and her confidence in me.

My gratitude goes to my supervisor Prof. Dr. Robert Weibel, for his invaluable help and expert advice in the field of GIScience and for the pleasant meetings throughout the past year. Without him, I would not have had the possibility to conduct the thesis in this interesting interdisciplinary field.

Further, I would like to express my gratitude to the following people:

- Stefan Graf, for explaining and discussing with me his extensive previous master thesis on which my work was then built. His R code saved me many hours of finding answers on Stack Overflow.
- Emma Lokuciejewski, who shared her ecological expertise and parts of her R code with me.
- Flavia Mäder, for listening to my thoughts, her continuous encouragement, never-ending support, and proofreading this work.
- My friends and family for being there for me when I needed them and for proofreading this work.
- To all master students in Geography who shared a common goal in room Y23G10 at the University of Zurich. The past year was memorable, thanks to countless jokes and discussions during lunch and coffee breaks.
- To the research assistants who conducted the focal animal follows in the Sumatran rain forest, and to the people who worked hard to clean the data sets used in this work.

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List of Abbreviations

AIC	**A**kaike **I**nformation **C**riterion
ANOVA	**AN**alysis **O**f **VA**riance
CI	**C**onfidence **I**nterval
CV	**C**oefficient of **V**ariation
DJL	**D**ay **J**ourney **L**ength
DOP	**D**ilution **O**f **P**recision
eFAI	**e**xperienced **F**ood **A**vailability **I**ndex
ENSO	**E**l **N**iño-**S**outhern **O**scillation
FAI	**F**ruit **A**vailability **I**ndex
FL	**F**ound-to-**L**ost
FN	**F**ound-to-**N**est
hFAI	**h**abitat **F**ruit **A**vailability **I**ndex = **FAI**
ICC	**I**ntraclass **C**orrelation **C**oefficient
LRT	**L**ikelihood **R**atio **T**est
LMM	**L**inear **M**ixed-effects **M**odel
ML	**M**aximum **L**ikelihood
NL	**N**est-to-**L**ost
NN	**N**est-to-**N**est
NSD	**N**et **S**quared **D**isplacement
PVA	**P**opulation **V**iability **A**nalysis
REML	**RE**stricted **M**aximum **L**ikelihood
SI	**S**traightness **I**ndex
TDD	**T**otal **D**isplacement **D**istance
TEE	**T**otal **E**nergy **E**xpenditure
VIF	**V**ariance **I**nflation **F**actor
WSR	**W**ilcoxon **S**igned-**R**ank test

Chapter 1

Introduction

1.1 Motivation

Orangutans share 97.5 percent of their DNA with humans and are thus one of human's closest relatives (Grehan and Schwartz, 2009). They are the largest arboreal mammals on Earth and an important keystone species for biodiversity conservation. The only place where the three existing orangutan species are found is on the islands of Sumatra and Borneo (Nater et al., 2017). Orangutans are depicted as a flagship species in wilderness conservation campaigns to galvanize interest and promote action to fight deforestation (Jepson and Barua, 2015). The close relatedness with humans leads to emotional reactions in politics and the public (Jepson and Barua, 2015). Unfortunately, this has not saved the orangutans so far. The three existing species are still on the Red List of Critically Endangered Animals (Singleton et al., 2018) because habitat loss, fragmentation, and wildlife trade pose an imminent threat to them (Marshall et al., 2009b).

To save them from extinction, however, their behavior and ecology need to be understood (Russon et al., 2009). Orangutans develop slowly, reproduce at a slow rate and live at relatively low population densities. Their slow life histories make them particularly vulnerable to population decline as it takes them a long time to recover from threats like habitat loss or hunting (Marshall et al., 2009b). Therefore, Marshall et al. (2009b) conducted a Population Viability Analysis (PVA) for the orangutan populations on Borneo and Sumatra, where they adjusted a population model with different parameters for the intensity of human-induced threats and conservation and management efforts. One of the key findings was that a population needs more than 250 individuals to ensure long-term population stability. Moreover, factors such as large body size, slow reproductive rate, limited geographic area, and frugivory, which all apply to orangutans, were suggested to promote extinction (Marshall et al., 2009b). Especially, the orangutans on Sumatra are at risk of local extinction because fewer individuals live in less suitable habitats, and deforestation happens faster than on Borneo (Wich et al., 2003). Furthermore, the impacts of fragmentation and isolation result in a discrepancy between impairments and delayed reduction in population size (Marshall et al., 2009b). As soon as a population declines, it could already be too late to save the orangutans.

An animal's movement and use of space play a crucial part in its ecology. A complex network of individual, internal, and external factors influence where, when, and how an animal moves through its habitat. Ultimately, those factors are essential to understanding the ecological need of a particular species. For many species, and especially for orangutans, a crucial external factor is food availability in the habitat and fruit in particular. Orangutans feed mainly on fruit but also on flowers, leaves, other parts of the vegetation in their habitat, insects, and at times small mammals (Vogel et al., 2017). Therefore, they are responsible for a substantial portion of the seed dispersal and contribute to a healthy ecosystem (Chapman et al., 1994; Russon et al., 2009). However, all tropical forests show fluctuations in the abundance of fruit within and across years (Knott, 2005), but they also vary in the intensity of low and high fruit periods (Vogel et al., 2017). Orangutans have physiologically adapted to fruit availability fluctuations by minimizing energy throughput (Pontzer et al., 2010). Still, their large body, big brain, and arboreal lifestyle demand certain energy intake to cover daily metabolic requirements (Vogel et al., 2017). Hence, getting food efficiently is essential. By facing different food situations in various rain forests, orangutans have adopted their behavior with differing strategies, which affect the ranging and movement behavior (Vogel et al., 2017). Knowing how orangutans respond to environmental variation helps to build more informed models about their behavior and morphology (Knott, 2005).

With this thesis, I aim to gain new insights into the impacts of fruit and food availability on socio-spatial movement patterns by analyzing long-term movement data of the Sumatran orangutans (*Pongo abelii*) within the Suaq Balimbing population. Ultimately, this knowledge will also help to develop effective conservation strategies to protect the orangutan populations. The remainder of this Chapter 1 describes the orangutan's biology and socioecology, followed by the context of foraging behavior, fruit availability, and ranging behavior. Chapter 1 then concludes with the research gap and the research questions.

1.2 Orangutan biology and socioecology

Three different orangutan species live in various parts of the islands of Borneo (*Pongo pygmaeus*) and on Sumatra in Indonesia (*Pongo abelii* and *Pongo tapanuliensis*). On the two islands, various orangutan research sites exist (Figure 1.1) (Wich et al., 2009). Slow life histories characterize all species of orangutans, and five main age-sex classes can be distinguished. Females become sexually active and reproduce for the first time when they reach the age of 15 (Noordwijk et al., 2018). *Adult females* usually have one *dependent offspring* (i.e. infants) (Van Noordwijk et al., 2009) and the process of weaning starts around the age of eight years (Knott et al., 2009; Noordwijk et al., 2018). Furthermore, females are occasionally accompanied by a semi-independent offspring (juvenile or *independent immature*) that moves more independently and explores the forest solely. Adult females play an active role in the skill acquisition of their offspring (Mikeliban et al., 2021). Male orangutans show bimaturism with two distinct morphs for sexual maturity: *flanged males* develop prominent secondary sexual features (larger body size, cheek flanges, and throat sacs), whereas *unflanged males* lack these features and resemble adult females in shape and size (Kingsley, 1982; Mackinnon, 1974; Wich et al., 2009).

Orangutans are the largest mammals in the world that live predominantly arboreal (Thorpe and Crompton, 2009). Ground use is more common on Borneo, where tigers are extinct (Mackinnon, 1974; Thorpe and Crompton, 2009). In contrast, Sumatran orangutans are rarely seen on the ground, most likely due to the existence of Sumatran tigers (Ashbury, 2020; Morrogh-Bernard et al., 2009; Thorpe and Crompton, 2009). Orangutans are semi-solitary and form a fission-fusion social organization. This organization form means they meet at travel parties, for example, for mating, protection from harassment, or for the socialization of infants, which they then leave again (Van Schaik, 1999).

Only mothers and their dependent offsprings form long-term social units (Galdikas, 1985; Van Schaik, 1999) (Figure 1.2). However, females are philopatric, which means that they form clusters of overlapping home ranges, where they associate more with known maternal relatives than with unknown ones (Ashbury, 2020; Noordwijk et al., 2012; Singleton et al., 2009; Singleton and Van Schaik, 2002). On the contrary, adult males move within much greater ranges (more extensive than a single study area), where they search for sexually active females and forest parts with high fruit availability (Utami Atmoko et al., 2009). Flanged males use so-called long calls (long-distance loud calls) to attract females. In contrast, unflanged males must actively roam through an area in search of fertile females. Therefore, they cover greater distances (Dunkel et al., 2013; Utami Atmoko et al., 2009).

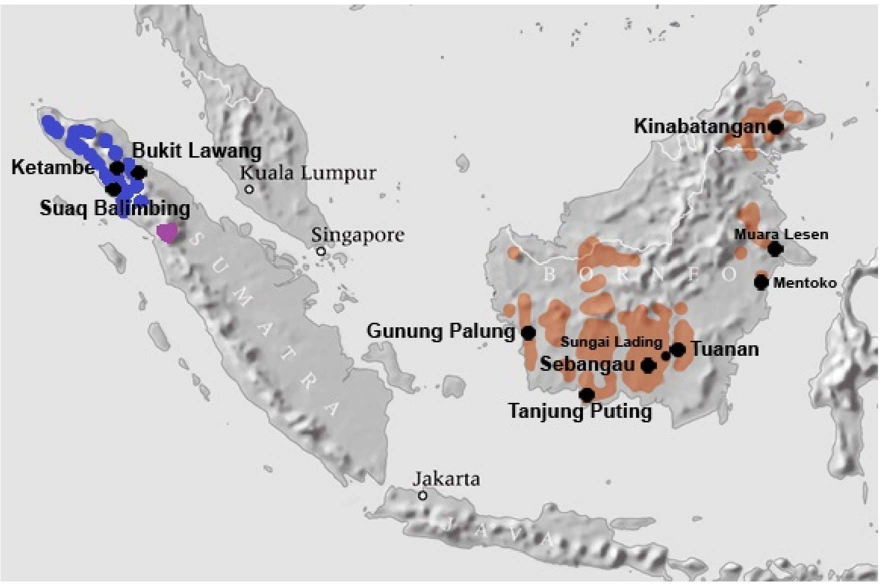


FIGURE 1.1: Locations of most of the research sites for orangutan studies on the website of the Orangutan Network (2021). Regions are colored in blue for *Pongo abelii*, in purple for *Pongo tapanuliensis* and in red for *Pongo pygmaeus*. *Source: Orangutan Network (2021).*

No discrete social communities (social units) could be distinguished among orangutans. Yet, they live in loose neighborhoods that consist of one or more female clusters, and in Sumatra, one flanged male that is preferred for mating. In these social networks, individuals exhibit – on spatial and temporal scales – preference and avoidance patterns with other orangutans. However, neither social nor spatial exclusivity is claimed (Setia et al., 2009; Singleton and Van Schaik, 2002; Van Schaik and Van Hooff, 1996). The orangutans' arboreal and limited gregarious lifestyle likely has positive effects on survival rates even though they live in a habitat with low plant productivity (Noordwijk et al., 2018).

Furthermore, orangutans are diurnal and build nests in the trees for the night. Building materials are small branches and leaves from which they make a sleeping platform for the night and sometimes for resting during the day (Prasetyo et al., 2009). In studies, data points from the morning and night nests are used to normalize the focal follows because they reflect their diurnal behavior and the movement between nests during the day.

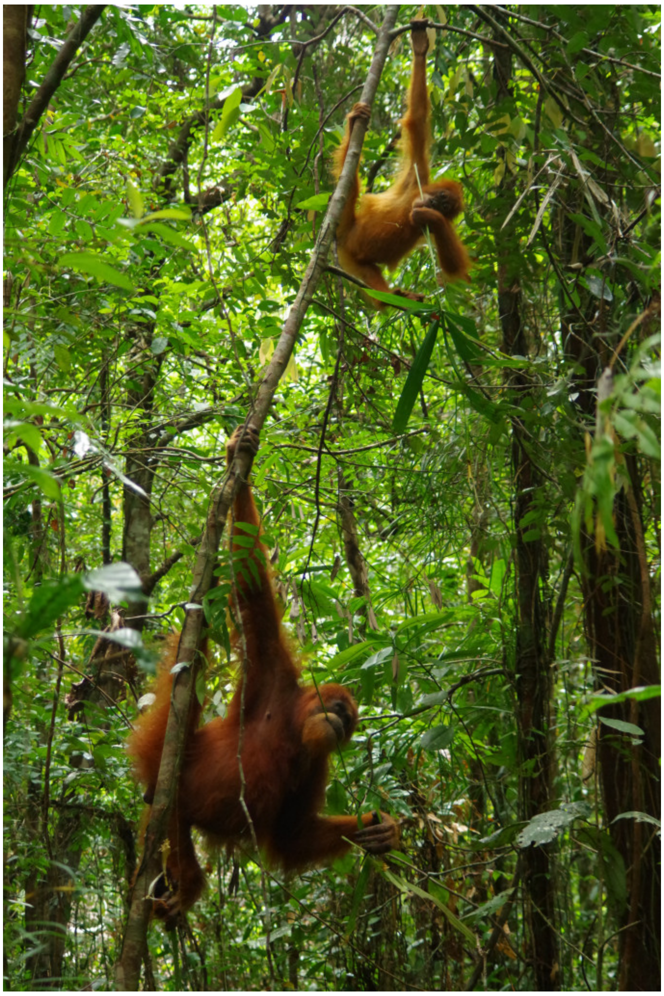


FIGURE 1.2: Photograph of female orangutan Lisa and her offspring Lois (*Pongo abelii*) in Suaq, Sumatra by Guilhem Duvot, 2017.

Geographic variation

As big arboreal mammals, orangutans require large amounts of calories and therefore spend around half of their day feeding (Knott, 2005; Morrogh-Bernard et al., 2009). Orangutan densities are strongly positively correlated with the quality and quantity of the forest's fruit production. Habitats that face less extreme variability of fruit support higher orangutan densities, for example, in the peat swamp forest of Suaq on Sumatra. On the contrary, orangutans living in fruit-scarce habitats generally have lower population densities, for instance, in the dryland dipterocarp forests of East Borneo (Husson et al., 2009; Marshall et al., 2009a). All orangutan species feed primarily on fruit, when available, but they further consume invertebrates, bark, flowers, and leaves, especially when fruit are scarce (Knott et al., 2009; Morrogh-Bernard et al., 2009).

Morrogh-Bernard et al. (2009) distinguished two different strategies of orangutan foraging behavior. The first one is used in forests with high fruiting seasonality and mast-fruiting (for example, in Gunung Palung on Borneo), and the second one in forests where a regular supply of fruit is present (for example, in Suaq on Sumatra). The strategy used in the first habitat type is referred to as 'sit and wait', whereas the one used in the latter is called 'search and find'. Further differences between the study sites are observed regarding social tolerance and social associations of orangutans, so-called parties. Between-site differences in fruit availability are assumed to influence the mean party sizes, whereas they are bigger in Suaq and Ketambe on Sumatra than on Borneo (Roth et al., 2020). Additionally, in Suaq there has been no observation of a significant temporal change in party sizes, which is possible because of a stable fruit availability (Van Schaik, 1999; Wich et al., 2006). Furthermore, orangutans show higher levels of social tolerance in Suaq than at other sites (Singleton and Van Schaik, 2002). This likely promotes a higher diet complexity (Schuppli et al., 2016a) and the use of tools in the foraging context (Meulman and Van Schaik, 2013).

1.3 Related work and research gap

1.3.1 Foraging behavior and fruit availability

Intake of energy from appropriate food is one of the basic life needs. Energy is needed for growth, reproduction, and repair (Pontzer et al., 2010). According to Pontzer (2017), the total energy expenditure varies relatively little within species but considerably between species, even when the effect of body size is considered. Fruit are the favored foods of orangutans (Knott, 2005) and are considered high-quality items (Marshall et al., 2009a). By mainly relying on fruit, orangutans can maximize their energy intake (Russon et al., 2009). However, rain forests worldwide do not constantly produce the food that orangutans prefer. All tropical forests that provide a habitat for apes are facing fluctuations in the abundance of fruit within and across years (Knott, 2005). Furthermore, there are great variations in the intensity of low and high fruit periods (Cannon et al., 2007; Vogel et al., 2017). In Africa, fruit availability varies within a year depending on the wet and dry seasons (Knott, 2005). On the contrary, the fluctuation of fruit availability in many Asian forests follows no strictly seasonal pattern but is triggered by climatic events once every two to ten years (Ashton et al., 1988). In general, Asian rain forests are less productive than African ones. However, they have greater interannual variations with so-called masting events, where super-abundance of fruit and periods of very low fruit availability take turns (Knott, 2005). In addition, there are also differences between Asian rain forests depending on the composition of the vegetation, the general habitat productivity, and the altitude (Russon et al., 2009).

Williamson and Dunbar (1999) have described the main daily activities of primates as feeding, resting, traveling, and socializing. Standardized field methods allow comparisons between different research sites on Sumatra and Borneo. In a study for multiple research sites on both islands, Morrogh-Bernard et al. (2009) found that orangutans spend most of their day feeding. Orangutans have adopted their foraging strategies to fruit availability variations. In Sumatran swamp forests, for example, they spend a major part of their day searching for fruit because throughout the year, they face a relatively steady fruit availability (Morrogh-Bernard et al., 2009).

Orangutan populations on Borneo, however, follow another foraging strategy, where they spend a lot of time resting and less time feeding to minimize their energy expenditure because they face mast-fruiting events and irregular fruit availability (Marshall et al., 2009a; Morrogh-Bernard et al., 2009). Yet, even for different Bornean research sites, varying results depend on the environment. In a study by Harrison et al. (2010) in the non-masting Sabangua peat-swamp forest, daily energy intake and fruit availability were positively related for flanged males but not for females or unflanged males. This could be a hint that age-sex classes differ in their foraging strategies, and fruit availability might not always be an accurate indicator of energy intake (Harrison et al., 2010). These differing strategies show that it is crucial to understand orangutan diets and foraging strategies to make factual statements about their biological adaptation and how their distribution and behavior are affected by ecological conditions (Russon et al., 2009). A comparable orangutan study even showed that orangutan densities are higher in places that are characterized by less extreme periods of food scarcity (Husson et al., 2009).

The spatiotemporal variation in fruit availability can substantially change behavior and physical conditions. Changes are, for example, shifts in ranging patterns, reproductive seasonality or vulnerability to predation, or changes in feeding efficiency (Vogel et al., 2017). Therefore, scientists have represented the fruit availability of a habitat in a specific measure. In ecology studies, this measure is called Fruit Availability Index (FAI) (Wrangham et al., 1998). The index is calculated as the percentage of fruit-bearing trees in an animal's habitat, here for orangutans, in a specific month (Wrangham et al., 1998). In research, the FAI has been used to explain variation in movement parameters, such as day journey length (Ashbury, 2020; Singleton et al., 2009; Vogel et al., 2017), inverse straightness index (Schuppli et al., 2016a), and the sinuosity index (Graf, 2021). I discuss the results of those studies and the descriptions of the parameters in the following sections.

1.3.2 Movement

Many studies in the past have focused on the home ranges of orangutans and their determinants over extended periods (Campbell-Smith et al., 2011; Singleton and Schaik, 2001; Wartmann et al., 2010; Wich et al., 2009). However, analyzing and modeling daily movement parameters was the objective only in some studies, even though they are necessary for the appropriate representation of seasonal feeding behavior (Ashbury, 2020; Graf, 2021; Wartmann et al., 2010).

Orangutans construct a nest every evening to spend the night in (Prasetyo et al., 2009). This behavior allows researchers to follow them from morning to night nest. Those nest locations represent the end points of the daily movement of this species, denoted as the Day Journey Length (DJL). Rowcliffe et al. (2012) described this DJL as a useful ecological variable because it links together the energetics, demography, and behavior. However, the authors criticized the underestimation of daily travel distances due to low sampling rates. Differences in DJL are often connected to changing foraging strategies (Campbell-Smith et al., 2011; Wich et al., 2009).

Generally, there is a link between total distance traveled and energy expenditure in orangutans (Knott et al., 2009). Graf (2021) analyzed DJL in Suaq. Monthly changes in DJL did not directly correlate with the FAI in the habitat. Vogel et al. (2017) analyzed the relationship between the FAI and DJL in Tuanan on Borneo. Contrasting the results from Suaq, they found that orangutans spent more time traveling, covered greater distances, and spent less time feeding when fruit were abundant, and they could increase their calorie intake. Knott (2005) has also demonstrated this pattern in another Bornean population. Furthermore, Wartmann (2008) found large differences between individuals regarding the total displacement distance and DJL. However, FAI had a positive effect on the DJL in Tuanan.

Other movement parameters are related to the tortuosity of the traveled route of an animal. First, the simple Straightness Index (SI) is one sinuosity value that reflects how direct or straight an animal's route is by dividing the DJL by the direct Euclidean distance from morning to night nest, which is also referred to as the Total Displacement Distance (TDD) (Schuppli et al., 2016a). SI can be used to study the foraging strategies or ranging behaviors in orangutans because it shows the directness of the movements in the travel route (Benhamou, 2004). Wartmann (2008) concluded that female orangutans in Tuanan on Borneo varied their travel distances according to seasonal changes in fruit availability. In contrast, another study in Sumatra did not find any correlations (Wich et al., 2006). Second, the sinuosity index (Section 4.1.1) is another value that is used to estimate the tortuosity of an animal's path and includes the average step length and the turning angles between consecutive GPS points (Benhamou, 2004). Graf (2021) showed that the FAI did not affect a change in the sinuosity of movement or the sinuosity between feeding trees in Suaq. However, the higher patchiness of feeding tree locations might lead to larger DJL (Graf, 2021).

1.3.3 Research gap

In the master's thesis of Graf (2021), no significant effect of the fruit availability on ranging patterns could be detected for orangutans in the Suaq research area on Sumatra. FAI did not impact DJL and had no significant effect on the sinuosity of movement or movement between trees. This result was rather astonishing as a great part of the daily life of orangutans is determined by feeding, and studies at other research sites had confirmed an effect (Vogel et al., 2017; Wartmann, 2008). However, one reason could be that at Suaq, orangutans do not face fruit scarcity and do not need to consume fallback food, which indicates that they are less energetically limited than their relatives on Borneo. Other reasons might be a study site difference referring to the structure of the forest or different behaviors of the orangutans. Furthermore, the FAI may not be a meaningful measure to assess the energetic state of the orangutans (Harrison et al., 2010). Consequently, a new approach could help to solve this discrepancy.

In an attempt to optimize the FAI, in Tuanan on Borneo an 'orangutan FAI' was calculated by including only tree species that are a part of the orangutan's diet (Knott, 2005; Vogel et al., 2017). Vogel et al. (2017) found that orangutans' intake of total energy and macronutrients varied with fruit availability. Additionally, the caloric intake was greater when the availability of fruit was high; however, this varied for age-sex classes (Knott, 2005). Nevertheless, no other study tried to devise an alternative index of fruit availability that would take the actual feeding behavior of orangutans, and its variation in time and space, into account.

Two limitations are crucial to understanding why a more sophisticated FAI would be helpful to explain movement parameters. Currently, the assessment of the FAI in the Suaq research area is based on two phenology plots with a north-to-south and east-to-west extent containing over 1000 trees, which are assessed once a month (Graf, 2021). FAI is a coarse measurement with one final number for the entire research area that does not represent spatial variation and experienced seasonality of fruit availability in much detail. Furthermore, all trees with fruit within these transects are included in the representation, but orangutans do not feed on all of them (Husson et al., 2009; Marshall et al., 2009a).

Therefore, to overcome this limitation and represent all food items orangutans feed on, this thesis aims at filling this research gap by introducing a new food availability index called the 'experienced FAI' (eFAI) and two sub-indices, which are based on this eFAI but split into a fruit and a non-fruit part. For future comparisons of orangutan study sites, it is essential to have a comparable measure of food availability, as no standardized method exists for expressing this variable (Morrogh-Bernard et al., 2009). With a better understanding and not only a temporal component but also a spatial one, an improved FAI may allow further and more differentiated insights into the movement parameters of the orangutans at Suaq and other sites. The eFAI may explain more variations in the movement parameters, such as the mentioned DJL or sinuosity index, than in the previous study by Graf (2021). Eventually, the proper quantification of consumed resources is essential for a better understanding of the ranging behavior and the protection of orangutans (Russon et al., 2009).

1.4 Research questions

In Suaq, the highest density of individuals was observed, and orangutans do not face any periods of fruit scarcity. The movement of orangutans is affected by the quantity and quality of food (Husson et al., 2009). However, the current indices used to assess food availability often only explain a small fraction of the variance seen in daily movement parameters, especially in Suaq on Sumatra compared to, for example, Tuanan on Borneo (Graf, 2021). Therefore, this thesis aims to analyze *behavioral data* and *waypoint GPS data* of Sumatran orangutans in Suaq (Section 2.2). Both data sets are collected in the field (Chapter 2) by following orangutans. However, in the former data set, for example, activity notes about feeding, moving, or resting are noted in intervals of 2 minutes. In contrast, in the latter, feeding events longer than 5 minutes and range points every 30 minutes are included with their coordinates. The first aim of the thesis is to establish a temporally and spatially more fine-grained index of food availability (eFAI) in contrast to the currently used FAI that represents the overall available fruit in the habitat. This eFAI is then split into a fruit eFAI and a non-fruit eFAI. In the former only fruit feeding points, and in the latter, only all other feeding points are included in the index. For a clear understanding, the traditional FAI is from now on referred to as 'habitat FAI' (hFAI), as it represents the quantity of available fruit in the habitat. Subsequently, the effects of food availability on the daily movement parameters of the orangutans, which were already addressed by Graf (2021) using the hFAI, will be repeated with the newly created eFAI, the existing hFAI and the two versions fruit eFAI and non-fruit eFAI.

The following questions are focusing on the representation of food availability in Suaq:

RQ A.1 *To what extent can an automated process of allocating feeding trees from the behavioral data to the waypoint GPS data replace manually collecting feeding tree locations in the field?*

The systematic mapping of resources during the focal follows in the *behavioral data* can help to support the manually set *waypoint GPS data* points in the field. In the first step of this thesis, the prediction is that an automated process for allocating feeding tree locations from this *behavioral data* to the *waypoint GPS data* can replace or at least complement the process of collecting feeding tree locations in the field. In that way, the GPS points from the field can be validated for completeness.

RQ A.2 *How can the representation of food availability be improved by including the actual locations of orangutan foods and their temporal use by the orangutans? How many follows per month are needed to reliably assess the eFAI, i.e., to reach a robust and thus representative value of the eFAI?*

Graf (2021) has shown that the existing hFAI did not explain a lot of the variation observed in the ranging behavior, despite having a significant effect at other sites, such as Ketambe on Sumatra (Morrogh-Bernard et al., 2009) or Tuanan on Borneo (Wartmann, 2008). The experienced food availability is directly calculated based on the collected *behavioral data* and the *waypoint GPS data*. It thus represents the food availability that the focal individuals experienced. Therefore, I predict that the eFAI can explain more variation in ranging behavior than the hFAI. However, this new index should be independent of the focal, and the variation in the eFAI values and their standard deviations should be minimized. My prediction is that a minimum number of follows per month – in the range of 5 to 10 – is needed to achieve the balance between being independent of orangutan individuals and follow days and experiencing too much data loss.

RQ A.3 *How does the hFAI value vary with time, and how does the eFAI value and its versions fruit eFAI and non-fruit eFAI vary with space and time in the research area? Do hFAI and eFAI relate to each other?*

My prediction is that there is an overall positive monthly correlation between the hFAI and the eFAI to a certain degree because orangutans can only experience the food that is also available in their habitat. I further predict that the eFAI shows spatial variation in the research area by providing information about hotspots and lower-density regions in food availability, which the hFAI cannot establish.

RQ A.4 *If food availability is split into a fruit and non-fruit eFAI component, how do they relate to the hFAI? What is the variation in the eFAI for a minimum feeding time of 30 minutes compared to 5 minutes?*

In the *behavioral data* information on feeding times is available. Therefore, I can test variations of the eFAI values for feeding points longer than 5 minutes. I predict that 30-minute feeding events give insights into finding relevant spots where orangutans preferentially feed. Furthermore, the hFAI only expresses the availability of fruit in the habitat. Therefore, it is reasonable to split the eFAI into a fruit and non-fruit component to assess the relationship between fruit eFAI and hFAI. Also, for the fruit eFAI, I predict a correlation to the hFAI to some degree because orangutans can only experience the fruit available in the habitat.

The following questions are focusing on orangutan movement in Suaq:

RQ B.1 *How do the four age-sex classes differ regarding the movement parameters?*

Based on the literature and the master's thesis by Graf (2021), I predict that there are differences in the movement parameters for the age-sex classes. Still, they are in accord with the average values of previous analyses (Graf, 2021; Singleton et al., 2009). I predict that DJL is higher for independent immatures and unflanged males than for flanged males and adult females. In contrast, I predict that the sinuosity is higher for independent immatures and unflanged males because they are expected to move more tortuous and less efficiently with less experience in the environment.

RQ B.2 *How are the movement parameters DJL, TDD, SI, and sinuosity index affected by hFAI, eFAI, fruit eFAI, and non-fruit eFAI?*

I predict that the eFAI and its versions, fruit eFAI and non-fruit eFAI, explain more of the variation in the movement parameters DJL, TDD, SI, and sinuosity of the travel routes than the hFAI because the new indices better represent the food availability that is actually experienced by the individual and not only what is available in the habitat.

1.5 Thesis structure

Chapter 2 gives information on the study area, the general methodology, and the data collection and preparation. Furthermore, it features an overview of the data that is then analyzed in Chapter 3. The creation and analysis of the new index eFAI and its two versions fruit eFAI and non-fruit eFAI in Chapter 3 is the first main contribution of this master's thesis and builds the basis for the second main contribution in Chapter 4. There, the focus is on the analysis and the effect of food and fruit availability on movement parameters, such as DJL, SI, or the sinuosity index. Therefore, both Chapters are divided into the specific methodology, results, and discussion parts, respectively. Those two main Chapters are then followed by the conclusion (Chapter 5), where the insights and major findings are listed, as well as explanations of the limitations of the used methods and possible perspectives for future work.

Chapter 2

General methodology and data preparation

This chapter presents details about the study area (Section 2.1) and shows how the data used in this thesis were collected (Section 2.2). The data pre-processing and processing workflow is described in Section 2.3. Section 2.4 shows the packages used with the programming language R, and Section 2.5 gives an overview of the data used in Chapters 3 and 4.

2.1 Study area

Behavioral data were collected in the study area of Suaq Balimbing (3° 42′ N, 97° 26′ E, approx. 75 m a.s.l.) located on the western coast of the Indonesian island of Sumatra in the area of Aceh Province (Figure 1.1). At this research site, the Department of Anthropology of the University of Zurich and the Max Planck Institute of Animal Behavior are conducting long-term studies about the behavior and movement of free-ranging orangutans. Research on orangutans started in 1992 but was halted from 1999 until 2007 because of political unrest in the province of Aceh (Wich et al., 2009). Nevertheless, research projects were resumed afterward. The research station next to a small river consists of small houses and serves as the entrance to the study site on the eastern side of the river. The area is best described as a mostly flat riverine peat swamp forest (Singleton and Schaik, 2001).

Suaq is situated close to the equator in a tropical forest, which infers a humid climate with less temperature variation throughout the year and more between day and night. The annual precipitation on site is around 3400 mm (Wich et al., 2009), which is in line with more recent data. However, the variation between years is high (Graf, 2021). Graf (2021) features a current overview of temperature, precipitation, and the weather phenomenon El Niño–Southern Oscillation (ENSO), which was shown to have an influence on mast fruiting events on Borneo (Russon et al., 2009). In contrast, Wich and Van Schaik (2000) and Graf (2021) showed that the influence of ENSO periods on mast fruiting events is weak on Sumatra.

Compared to other sites, for example, the selectively logged peat swamp forest in Tuanan on Borneo, the forest at Suaq is mainly undisturbed, with a larger density of huge trees (Manduell et al., 2012). Orangutan density in the Suaq research area is approximately seven individuals per km^2 and thus the highest of all orangutan populations (Singleton et al., 2009). Year-round, there is a high fruit availability. The soil is muddy, and numerous back swamps are frequently flooded, leading to an irregular forest structure (Singleton and Schaik, 2001). For easier ground movement in the area, a trail system was installed that represents a study grid made up of narrow paths, with one trail featuring a boardwalk constructed of wooden planks. The flat peat swamp forest continues to the north of the study area, up to the foot of the hills and mountains of the Leuser Range. The adjacent hills are characterized by a mixed dipterocarp forest (Singleton and Schaik, 2001).

2.2 Data collection

The overall workflow of this thesis includes data collection and processing, data modeling, and data visualization according to Wickham and Grolemund (2016). An overview can be seen in (Figure 2.2). The data sets used in this thesis are provided by the Development and Evolution of Cognition Research Group at the Max Planck Institute of Animal Behavior in Konstanz, Germany. Individual focal data were collected in accordance with standardized field methods (https://www.aim.uzh.ch/de/orangutannetwork/sfm.html). They consist of *GPS and observational data* of the Sumatran orangutans (*Pongo abelii*) at the Suaq Balimbing monitoring station from 2007 to 2021, collected in focal animal follows. *Observational data* is permanently stored in different tables of a Microsoft Access database, whereas the *GPS data* is stored in the GPX format.

An orangutan observed in the field is referred to as *focal*. Handheld GPS devices pinpoint the locations of the movement and feeding behavior in the peat swamp forest. The night nest from the previous day usually indicates the start point for the next follow. The behavioral data collection approach is strictly non-invasive and exclusively observational (Kunz et al., 2021; Schuppli et al., 2016a). The location below the animal is preferentially measured after the focal has moved on because the minimum distance of any observer to an orangutan should be 10 m to minimize human impact on orangutans (Kunz et al., 2021). Consecutive follows are restricted to at most ten days to minimize the risk of potential effects on the orangutans (Schuppli, personal communication, 2022). Therefore, focal selection may be influenced by previous follows, the distance to the research station, and the requirements of ongoing studies.

Graf (2021) already did a substantial amount of pre-processing of the *GPS data* for further analysis. However, new *observational data* from the database and *GPS data* from multiple years, including 2021, were added to the already existing and analyzed data. The *GPS data* was collected by researchers, trained field assistants, and students for around 180 individuals of all age-sex classes and 1879 follow days.

The *observational data* consists of the *behavioral data* (cf. exemplary Table A.1) and the *follow log data* (cf. exemplary Table A.2). The former includes the activities of the focal individuals, such as feeding, moving, and resting, that were recorded through scans at 2-minute time intervals (small green and orange points in Figure 2.1). Through these activity scans, the duration and food items of every feeding event can be accessed. The latter features a simple overview of all follows, including information on the length of the daily activity, the age-sex class, and the follow number.

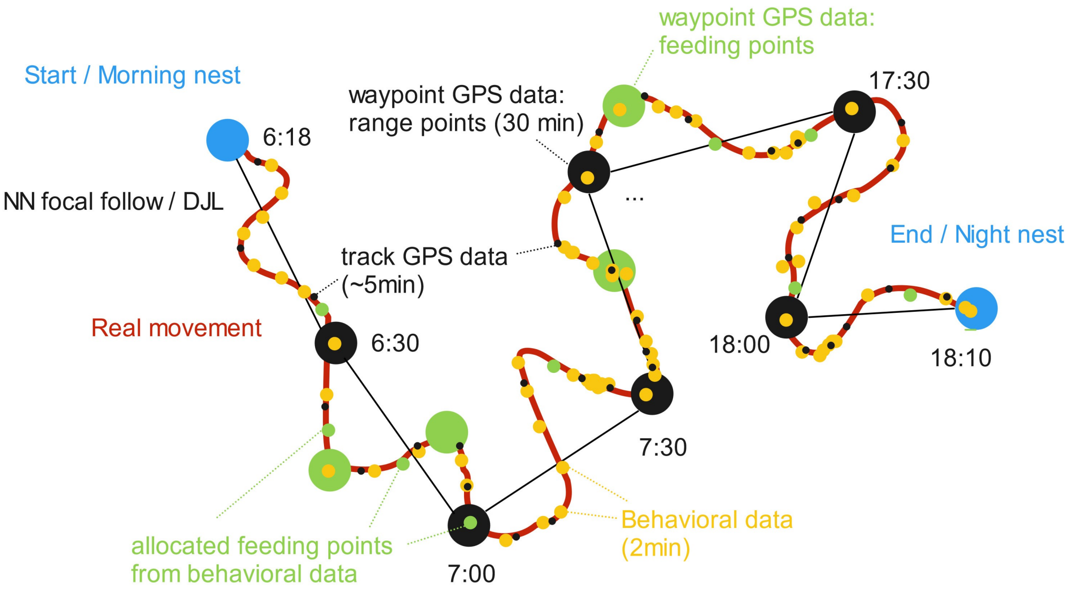


FIGURE 2.1: Schematic representation of a nest-to-nest (NN) focal follow in the field from a morning to a night nest. *Waypoint and track GPS data* are represented in black and the *behavioral data* in orange, whereas the real movement of an orangutan is drawn in red. The Day Journey Length (DJL) is derived from the black lines connecting the big black points. Big green points indicate the feeding locations, and the small ones represent the allocated feeding points from the *behavioral data*.

The *GPS data* consists also of two different data sets, the *waypoint GPS data* (cf. exemplary Table A.3) and the *track GPS data* (cf. exemplary Table A.4). In the *waypoint GPS data*, locations of the orangutans were taken every 30 minutes with GPS devices (Garmin models GPSMAP 62 s, GPSMAP 64s, and GPSMAP 78) during the focal follows and whenever the focal ate at a place for longer than 5 minutes (Schuppli et al., 2016a). Within this data, 30-min GPS points are referred to as *range points* (big black points in Figure 2.1), whereas the feeding GPS points are called *feeding points* (big green points in Figure 2.1). At every morning, day, and night nest, and when an orangutan is found or lost, additional GPS points are taken and tagged with the event. Range and feeding points are used to calculate the monthly eFAI in Section 3.1.2. The two versions fruit eFAI and non-fruit eFAI are calculated by only taking either fruit feeding points or all other feeding points in the respective formula. In the field, other GPS points are taken for social associations (so-called parties, defined by two or more orangutans being within a distance of at most 50 m of each other), for long calls, for tool use, or when fecal samples are collected. Those points are not of particular interest in this thesis. Additionally, in the *track GPS data* for many follows in the years 2013 to 2021, GPS points that were taken automatically by the device at a few seconds to usually 5-minute intervals are available (small black points in Figure 2.1).

Lastly, monthly (habitat) FAI values were used in the analysis. This index was measured as the percentage of trees bearing fruit in phenology plots of two transects in the study area containing over 1000 trees for each month (Marshall et al., 2009a).

2.3 Data pre-processing and processing

Various steps of data cleaning and preparation were needed to produce the final data sets used in Section 3.1.2. In the first step, I added information about the class and sex of the focal and the activity length from the *follow log data* to each data point in the *waypoint GPS data* (Figure 2.2). I divided orangutans into five age-sex classes: adult females, flanged males, unflanged males, independent immatures, and dependent immatures. I did not include the age-sex class of dependent immatures (i.e., infants) in any of the analyses in this thesis as dependent immatures mainly follow their mothers. Thus, their movement parameters are unlikely to be directly influenced by external variables. Further, all GPS coordinates were reprojected from the WGS84 (EPSG: 4326) coordinate system to the local national spheroid DGN95/UTM zone 47N (EPSG: 23867) with Cartesian coordinates. Thereby, the timezone was defined as Asia/Pontianak (UTC+7).

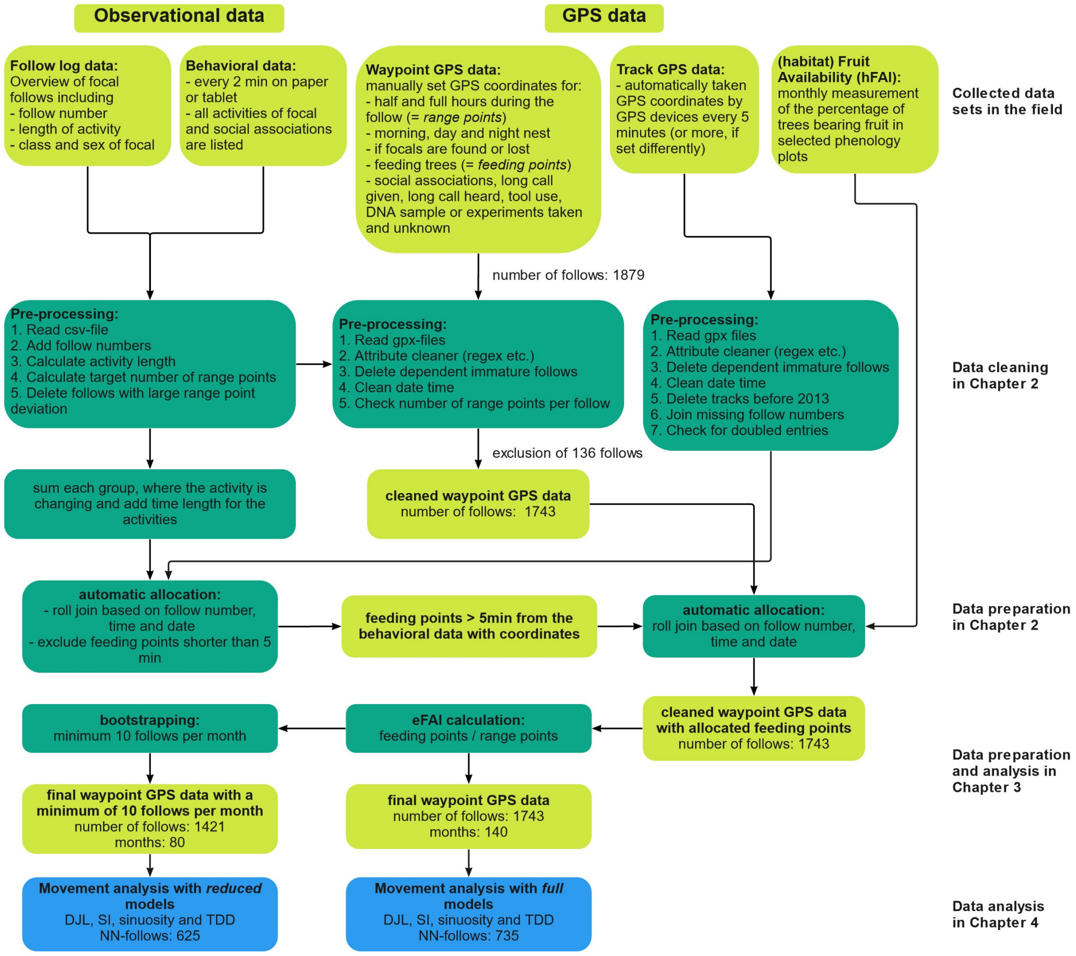


FIGURE 2.2: Workflow overview from data collection, pre-processing, processing to the final data analysis.

I tested each focal follow in the *waypoint GPS data* for completeness by calculating the number of 30-min range points (all big black points in Figure 2.1). I excluded focal follows that did not contain range points from the analyses because I assumed that these follows were too short or that their data were faulty. Furthermore, I estimated a target number of range points in the *behavioral data* by summing the length of the activity (all small orange points in Figure 2.1) and dividing it by 30. I then compared this number to the 30-min range point number in the *waypoint GPS data*. Focal follows with a deviation that was above or below a defined threshold (+4 and -2) were manually checked and, if necessary, omitted (Figure A.1). Based on the data cleaning, I excluded 136 follows. Furthermore, I corrected inconsistencies in the *behavioral data*, in the *waypoint GPS data* and the *track GPS data*.

To increase the completeness of the feeding points in the *waypoint GPS data*, all feeding events recorded in the *behavioral data* of each follow were matched with and allocated to the former data (Figure 2.2: data preparation). To achieve this I first assigned the *behavioral data* to the temporally closest GPS point in the automatically collected *track GPS data* to get information about the location of the feeding event. I excluded feeding points shorter than 5 minutes per definition as they are not set in the *waypoint GPS data* (Schuppli, personal communication, 2021). Then, I matched and allocated feeding points in the *behavioral data* with coordinates to the *waypoint GPS data* based on their time, date, and follow information. If those criteria matched, I created no additional feeding point in the *waypoint GPS data*. However, if the feeding point was new, I included it in the *waypoint GPS data* as an additional point. The results of this allocation process are noted in Section 3.2.3. Furthermore, I calculated the distance deviations of matching feeding points to validate the positions of the orangutans in the field (Section 2.5: GPS accuracy). Then I checked and corrected the final *waypoint GPS data* for inconsistencies and added monthly hFAI values to each follow.

2.4 Software

For all steps in the workflow of data processing, analysis, and visualization, I used the integrated development environment (IDE) RStudio (2021.09.0+351) for the programming language R (4.1.1) (R Core Team, 2021). In Table A.5, relevant packages used in data processing and calculation of the eFAI (P/eFAI) and the analysis of daily movement (MA) are listed. The complete R code scripts and the movement analysis results can be requested and provided with the data manager's permission (Dr. Caroline Schuppli).

2.5 Data overview

The following data overview is derived from the data pre-processing and processing described in Section 2.3. As will be reported in Section3.1.2, I processed this data then further to find a minimum number of 10 follows per month that I used in the analysis reported in Chapter 3 and 4. Finally, I used both data sets in the linear mixed-effects models shown in Section 4.1.3 for comparison and interpretation purposes.

There is a lot of variation over time in terms of the number of follows and the amount of data collected per month. The spatial data is unbalanced regarding age-sex classes and focal sampling effort. In total, there were 1743 follows with GPS data available (adult females: n = 648; flanged males: n = 461; independent immatures: n = 320; unflanged males: n = 314), stemming from 138 individuals. However, around 27% of the data comes from the four adult females that were followed most frequently. Figure 2.3 shows the distribution of the follows over different years and months. The fact that more follows exist for adult females and flanged males during certain periods relates to the particular study goals of the researchers.

FIGURE 2.3: Overview of the number of follows per month for each age-sex class. The imbalance of follows for age-sex classes stems from particular study goals of the researchers at the Suaq station and the orangutans that were actually found in the area.

The data used in this thesis were collected from 2007 to 2021, corresponding to 14 years and five months. Research activities are still ongoing. Focal follows are divided into different follow types that represent where follows started and ended. The follow types are nest-to-nest (NN), found-to-nest (FN), nest-to-lost (NL), and found-to-lost (FL). The mean follow duration for NN follows was 11:04:30 hours (n = 771). For FN follows the average was 04:48:54 hours (n = 632), for NL follows 06:03:25 hours (n = 220) and for FL follows 03:25:56 hours (n = 120) (Figure A.2). A Kruskal-Wallis test of the NN follow duration suggests a significant difference between the age-sex classes (df = 3, χ^2= 8.485, p = 0.037). However, a non-parametric Wilcoxon rank-sum post hoc test with corrections for multiple testing according to Benjamini and Hochberg (1995) shows that there is only a trend and no significant difference between flanged males and the other age-sex classes (WRS, p = 0.064). Furthermore, Figure A.3 shows a similar activity duration distribution for NN follows. Nevertheless, flanged male duration density distributions seem to be visually different from the other age-sex classes (Figure A.3).

Various factors can influence data quality for the subsequent analysis, including, for example, the GPS accuracy, the sampling interval of the data points, and the researcher bias. Graf (2021) has already given insights into those factors based on a similar data set from the same research area. Therefore, I only mention them briefly here. More detailed information is found in Chapter 2.2 of the master's thesis by Graf (2021).

GPS accuracy

Graf (2021) has mentioned that the GPS devices used (GPSMAP 62s, GPSMAP 64s, and GPSMAP 78) do not provide any dilution of precision (DOP) information, which is used to describe the vertical, horizontal, positional and temporal accuracy of a device (Langley, 1999). However, an accuracy value is displayed on the screen, and in the manual of the GPSMAP 62s, the horizontal positional error is described as lower than 10 m in 95 % of cases. Research assistants in the field do not write down any accuracy value. Nevertheless, they are instructed in the data collection protocol to wait until the displayed accuracy value is below 12 m.

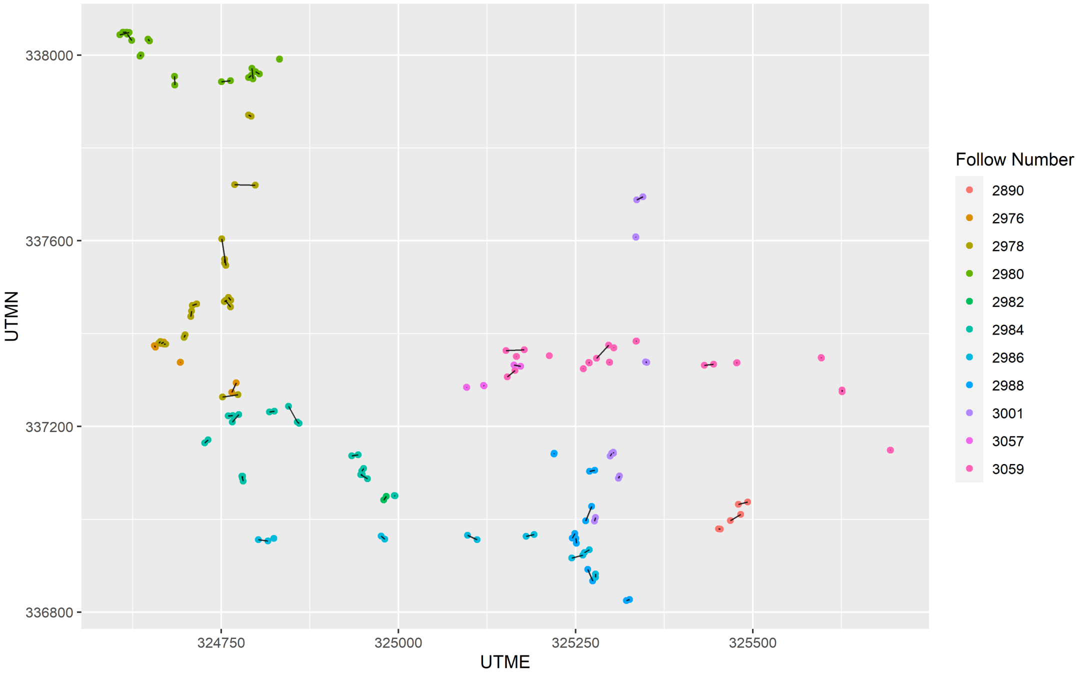


FIGURE 2.4: Feeding points in the *behavioral data* and *waypoint GPS data* for focal Friska in the year 2020. Manually and automatically set GPS coordinates are compared, and distance deviations are calculated. Matching feeding points are shown with black segments in this plot ranging from 0.23 m to 57.56 m.

In this thesis, I compared GPS coordinates from feeding events recorded in the *behavioral data* and feeding trees in the *waypoint GPS data* (Section 3.2.3). I then looked at the distance deviations of the manually taken and automatically assigned GPS coordinates of the same feeding trees. Figure 2.4 shows a visual example of the focal Friska (the individual with the most follows and longest tracking history) in 2020 and her feeding coordinates as they are compared with each other. For all orangutans and the whole research period, I could match 4280 feeding points and calculate the distance between them. In Figure A.4, a right-skewed distribution indicates that many follows have a low distance deviation. Only seven feeding trees had a distance deviation greater than 100 m. Overall, I detected a mean value of 10.95 m, which is similar to the mean positioning error (9.8 m) of Wartmann (2008) for the research site Tuanan on Borneo, and within the accuracy figure given in the technical documentation of the GPS devices used (see above).

Sampling interval and researcher bias

The analysis of movement in Chapter 4 can be influenced by irregular sampling intervals, which can lead to an underestimation of movement parameters (Calenge et al., 2009). Graf (2021) checked if his data, which is partly also relevant for this thesis, needed a sampling harmonization. He mentioned several methods that could be used but decided against sampling harmonization because the advantages were outweighed by the loss of information, the complexity of the method, and the introduction of new biases. Furthermore, the amount of irregularities in the sampling interval of the data is low (Graf, 2021).

Additionally, a possible observational bias by researchers was analyzed (Graf, 2021) taking into account the trail system in the study area and the follow's start and end points. Graf (2021) concluded that start points are somewhat biased by the research transects, but the end points of follows, and the total number of GPS points are biased as well, whereas there is no apparent bias towards the research station. However, these effects were much smaller than in the study of Wartmann (2008) and do not play a significant role in the analysis of DJL or the creation of the new index eFAI in this study, as I am looking at the total daily movement of orangutans and not only at their start or end points.

Chapter 3

Fruit and Food Availability in Suaq

3.1 Methodology

3.1.1 Habitat FAI (hFAI)

Habitat FAI (hFAI) values were taken monthly based on counts and observations of researchers on fruit-bearing trees in two transects of the research area. hFAI is commonly used under the name FAI in various studies as an explanatory variable (Ashbury et al., 2020; Graf, 2021; Singleton et al., 2009; Singleton and Schaik, 2001; Vogel et al., 2017). It indicates the ratio of the number of fruiting trees compared to the total number of trees as a percentage resulting in one single number for the whole research area per month. In Sections 1.3.1 and 1.3.3, I mentioned that this fruit availability estimate could be replaced by a new index called eFAI in the research area of Suaq.

3.1.2 Workflow - eFAI

eFAI calculation

The full data set described in Chapter 2, where additional feeding tree points from the *behavioral data* were joined to the manually collected *waypoint GPS data* during the focal follows (Figure 2.1), was used for the calculation of the eFAI values. In a first step, I define the eFAI as the *experienced food availability* in the habitat of all the orangutans over a month or in a spatial grid cell in the research area (Section 3.1.2: Spatial variation). It is based on all the consumed food and is derived from the ratio of the total number of feeding points in the data to the total number of range points taken systematically every 30 minutes. Thus, the data is normalized to account for focal follows with varying observation lengths (Figures A.2 and A.3). A higher eFAI value means that orangutans were feeding at more places for longer than 5 minutes during a month. Values greater than 1.0 are obtained when more feeding points are noted than standardized 30-minute points.

In the data, inconsistencies in the number of range points existed. Yet, these standardized points at 30-minute intervals are essential for calculating the eFAI, which made the preprocessing step of cleaning follows necessary (Section 2.3). Consequently, I computed eFAI values from the available data that is also used to derive movement parameters, for example, the DJL and the sinuosity index (Section 4.1.2). Nevertheless, this measure is not based on the preference of a single orangutan or day. Instead, it is an independent estimate corresponding to a general feeding behavior that should reflect the experience of available food during a month or in a specific area. As the number of follows per month is limited, it was impossible to include the temporal and spatial components simultaneously.

Bootstrapping: Determining the minimum number of follows per month needed

The eFAI is based on various focal follows and days. However, these follows can vary in the number of feeding trees or range points and lead to different values of the eFAI, depending on which follows are taken. A greater sampling size automatically includes follows from different focals because they are not tracked for longer than a few days. To account for the effects of sampling variation and to ensure independence from one specific focal, I calculated the minimum number of follows needed per month with bootstrapping, a method of random resampling with replacement. This statistical method is used where only a single sample is available (Efron and Tibshirani, 1993). The idea of bootstrapping is to create many simulated samples by resampling a single data set and thereby constructing the bootstrap distribution, which corresponds to an approximation of the sampling distribution (Kulesa et al., 2015). Additionally, it is used to estimate confidence intervals, standard errors, or for hypothesis testing (Efron and Tibshirani, 1993).

For each month, I had 3 to 36 follows available and computed 100 iterations of bootstrapping resampling with replacement to calculate eFAI values. Mean values, standard deviations, and the 95% confidence intervals (CI) were retrieved and used to find a minimum number of follows per month where the coefficient of variation (CV) (Abdi, 2010) is minimal. The CV indicates the degree of precision in the data, and good values for the CV vary depending on and within the field of research. In field experiments in agriculture, for example, the acceptable range is around 6 to 15% (Gomez and Gomez, 1984), whereas much lower CVs are common in medicine.

Additionally, I compared this approach to the CI. However, CI is calculated partly based on the standard deviation and the mean and was, therefore, not chosen as a criterion to determine the minimum number of follows needed to calculate the eFAI. Consequently, I identified a saturation level of a minimum number of follows per month to ensure a certain level of robustness of this newly computed index. I rejected a higher cutoff as this would have resulted in the loss of data (i.e., months). Therefore, I omitted all months containing fewer focal follows than 10 for the main analysis for Chapter 4. However, for completeness, results from the analysis with all the months were included in the Appendix to show trends for the whole data set without any restrictions to a minimum number of follows.

Versions of eFAI and comparison to hFAI

In this thesis, I computed different versions of the eFAI value. First, I calculated an eFAI value based on fruit feeding points only, that is, a *fruit eFAI*. The fruit eFAI should be most similar and thus comparable to the hFAI because the hFAI is inferred from fruit-bearing trees only (see above). Likewise, I created a *non-fruit eFAI* to complement the fruit eFAI. Second, in addition to using a 5-minute cutoff of feeding time, I calculated a *30-minute eFAI* (i.e., locations where the focal individual fed for at least 30 minutes). The 30-minute feeding points should indicate essential feeding locations and hotspots of food. However, the initial *waypoint GPS data* does not include information on the feeding length at the respective points; only the allocated feeding points from the *behavioral data* do (Section 2.3). Therefore, I could not detect all of the 30-minute feeding points. This statistic needs, therefore, to be interpreted with caution. Nevertheless, I compared all computed monthly eFAI values, the fruit eFAI, and the 30-minute eFAI to hFAI values, and I tested correlations and displayed them (Section 3.2.5). Furthermore, I compared the fruit eFAI to the non-fruit eFAI and tested the correlation.

Spatial variation

I represented the spatial variation of the eFAI values by calculating the overall eFAI for hexagonal grid cells of 500 meters in size between parallel sides. A simultaneous spatial and temporal comparison of eFAI values with the cleaned *waypoint GPS data* and a minimum of 10 follows per month was only possible by analyzing some years together. I always separated three consecutive years for the research period from 2007 to 2021 and then compared them. Figure B.7 C shows that approximately always after three-year periods of high data density, no eFAI data is available for some months because these months have less than 10 follows. Additionally, in that way, several fruit cycles on Sumatra can be included in the analysis, as can be seen, for example, in Wich et al. (2011). Furthermore, I represented the fruit eFAI and non-fruit eFAI in the grid cells to look into regional differences between the fruit and non-fruit diet of orangutans. I chose hexagonal grids for all representations because they are more circular than squares and more suitable when representing the movement paths or connectivity of different cells in ecology (Birch et al., 2007). A hexagonal grid of 500 meters allows us to see small-scale, rather fine-grained variations in the research area. Simultaneously, it includes sufficient GPS locations to make a statement about the differences between cells.

I calculated χ^2-statistics for the spatial variation of feeding places over the research area. Pearson's residuals were retrieved by comparing the expected versus the observed values of feeding points (Equation 3.1). The observed values were given by the number of feeding places in a particular cell. I computed the expected values for each research period based on the corresponding ratio of feeding points to range points (which represent the overall follow effort in the area) as they are positively correlated (Figure B.1). Additionally, I calculated mean values with standard deviations. These values allowed me to see where more or less feeding places occurred than were expected. I used the following equation to calculate the Pearson residuals:

$$r_k = \frac{O_k - E_k}{\sqrt{E_k}} \tag{3.1}$$

where r_k is the Pearson residual for cell k with O_k as the observed value for the cell and E_k as the expected value for the cell.

3.2 Results

3.2.1 Food locations in Suaq

Based on the months with a minimum of 10 follows, I retrieved the coordinates of all feeding points (Section 3.2.3). Figure 3.1 shows their spatial distribution in the research area. In the middle of the research area, more feeding locations are found than near the borders in the East and North. Those locations are further away from the research station. An analysis of the expected versus the observed number of feeding trees (Section 3.1.2) shows a similar picture.

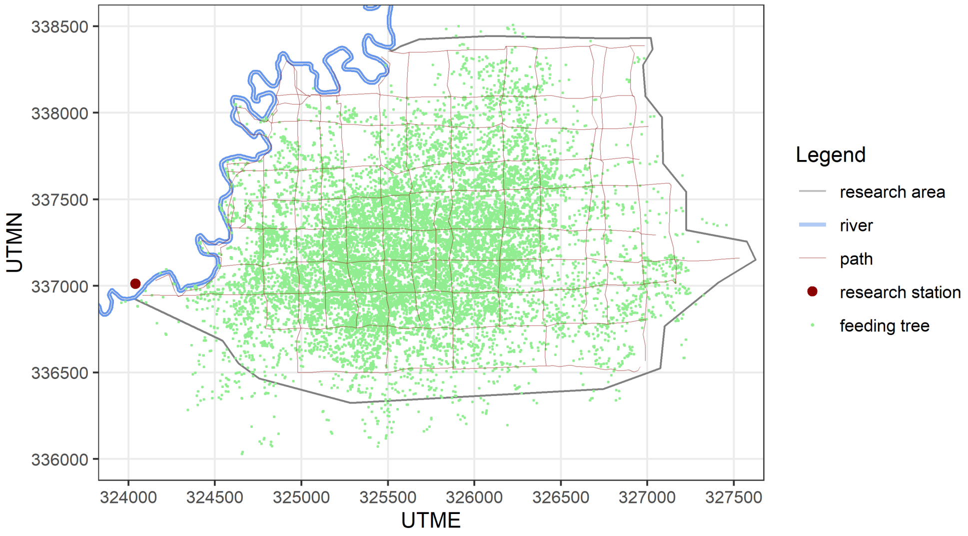


FIGURE 3.1: Spatial distribution of feeding trees in the research area.

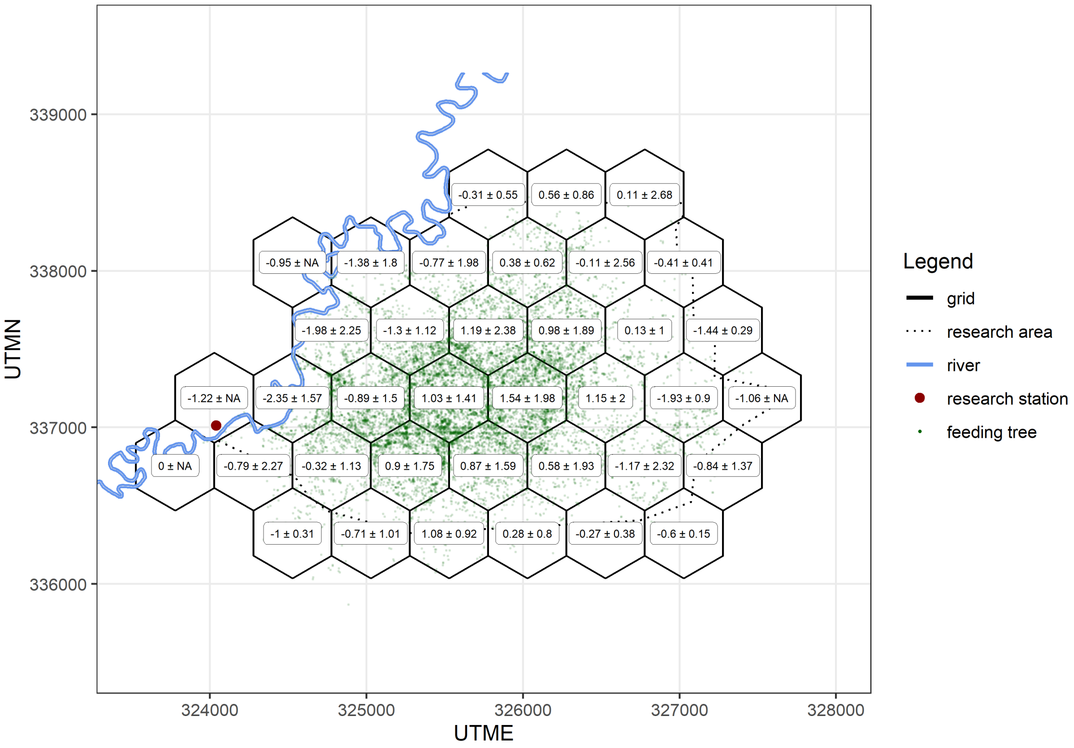


FIGURE 3.2: Mean and standard deviations of the Pearson residuals of feeding points in hexagonal grid cells of 500 m. Positive numbers indicate that more feeding events were observed than expected, whereas negative numbers show fewer feeding events. NA values occurred if the specific cell only contained information from one research period. In such cases, it was not possible to calculate standard deviations.

Pearson's residuals from the χ^2-statistics for three-year research periods demonstrate that more feeding trees are observed in the core and the South of the research area than expected, indicated by positive numbers in Figure B.2. Negative Pearson residuals are found more often in the South-East, in the East, and along the river near the research station, indicating fewer feeding trees than expected. Mean and standard deviations of the Pearson residuals in Figure 3.2 show these trends. However, the variation between the different analyzed periods is large. Similar trends were found for the fruit locations (Figure B.3), whereas the non-fruit locations showed more negative and positive variations of the Pearson residuals in the core cells (Figure B.4).

3.2.2 Bootstrapping: Determining the minimum number of follows per month needed

As an example, Figure 3.3 shows the bootstrapping results for all months in year 2020 and for sample sizes from 3 to 36. In Figure B.5, a more detailed overview with mean values, standard deviations, and CI is given. Generally, standard deviations and CI decrease with larger sample size. There is a clear variation in the average eFAI values for the different months, ranging from 0.2 to 1.23 (mean = 0.80, sd = 0.18). In the year 2020 the variation is smaller, yet still ranging from 0.53 to 1.03 (Figure 3.3).

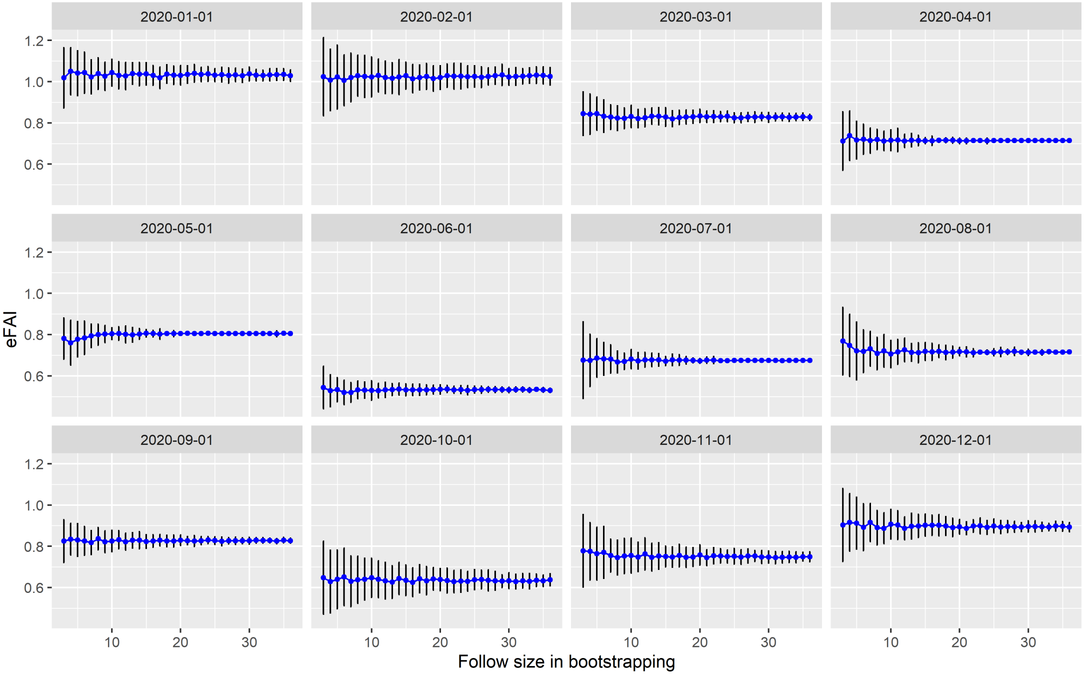


FIGURE 3.3: eFAI calculation and bootstrapping for all months in the year 2020. For each sample size from 3 to 36, mean values are indicated by a blue dot and connected with a blue line. Black error bars show the corresponding standard deviation.

I took the coefficient of variation below a threshold of 10% to find a minimum number of follows needed per month for further analysis. I observed a mean value of 8.19 (Figure B.6). Tests with threshold values of 5% and 20% for the CV show, on average, a minimum of 16.57 follows per month needed for the former and 3.85 for the latter. Conservatively, for further analysis, I defined a threshold of 10 follows per month for an acceptable robustness of eFAI values. Consequently, after this step, the data of the included months was reduced from 140 to 80. For every year, except for 2012 (as no months featured a minimum of 10 follows), I analyzed at least some months in Section 3.2.5.

3.2.3 Allocation and matching of feeding points

To complete the feeding tree GPS points (Section 2.3), I allocated the feeding points retrieved from the *behavioral data* to the initial *waypoint GPS data*. This allocation procedure changed the result of the eFAI calculation significantly. A visual comparison of the eFAI over time (Figure B.7) shows (A) differences for many months for the initial *waypoint GPS data*, (B) the *waypoint GPS data* with additional feeding points from the *behavioral data*, and (C) for a minimum number of 10 follows per month based on the bootstrapping. The change was most pronounced from 2013 to 2015 and in 2017 (A), where the initially calculated eFAI values were around 0 to 0.2, suggesting that many feeding points were missing and probably not recorded in the field. The eFAI values increased after adding the feeding trees based on the *behavioral data* (B). On the contrary, the temporary spikes of eFAI at the end of 2010 and the beginning of 2011 decreased after data cleaning and the allocation process (B). Furthermore, this new, more complete data set shows that for most months, eFAI values range between 0.5 and around 1.0 compared to a larger range and more clumps in the initial data set (A). Long lines in (C) indicate missing months with less than 10 follows for 2009 - 2013 and 2014 - 2017. Since 2017 more than 10 orangutans have been observed in the majority of months.

For manually set feeding points in the field (in the *waypoint GPS data*) and *behavioral data* feeding points, I calculated the distance deviations between the two point types. In Section 2.5, I retrieved a mean deviation of 10.95 m for all of these comparisons. During the allocation process, I added 10,493 new feeding points for all months with a minimum of 10 follows (Section 3.2.2), of which 8,065 have information on their coordinates. All these points correspond to a feeding length greater than 5 minutes that were not included in the *waypoint GPS data* before. If the feeding time cutoff is raised to 30 minutes, I could only add 1,517 feeding points.

The number of feeding points added per month, but corrected for the respective number of follows (= ratio of the number of feeding points to the number of follows per month), was on average 7.37 ±4.25. Values didn't follow a normal distribution, but there was no systematic difference for specific months (Kruskal-Wallis, df = 11, χ^2 = 2.94, p = 0.99). On a yearly basis, the average of added feeding points per follow was 7.49 ±3.67. Values on a follow basis varied from 1.18 in 2021 to nearly 12.93 in 2015.

3.2.4 What do the orangutans at Suaq eat?

The monthly percentage of fruit points of the total number of feeding points where orangutans were eating varied throughout the study duration. Figure 3.4 shows the percentages over the months and years. The average was 61.6 ±11.58%, and values range from 29.66% to 85.35%. Furthermore, 30-minute feeding points as a percentage of the total number of feeding points varied from 6.01% to 40.4% (mean = 16.79 ±6.80). I detected no correlation between the percentages of fruit points and 30-minute feeding points (Spearman's rho, $r_s = 0.044$, $p = 0.70$). Values for months with less than 10 follows are not included in this analysis, based on results of the bootstrapping resampling with replacement (Section 3.2.2).

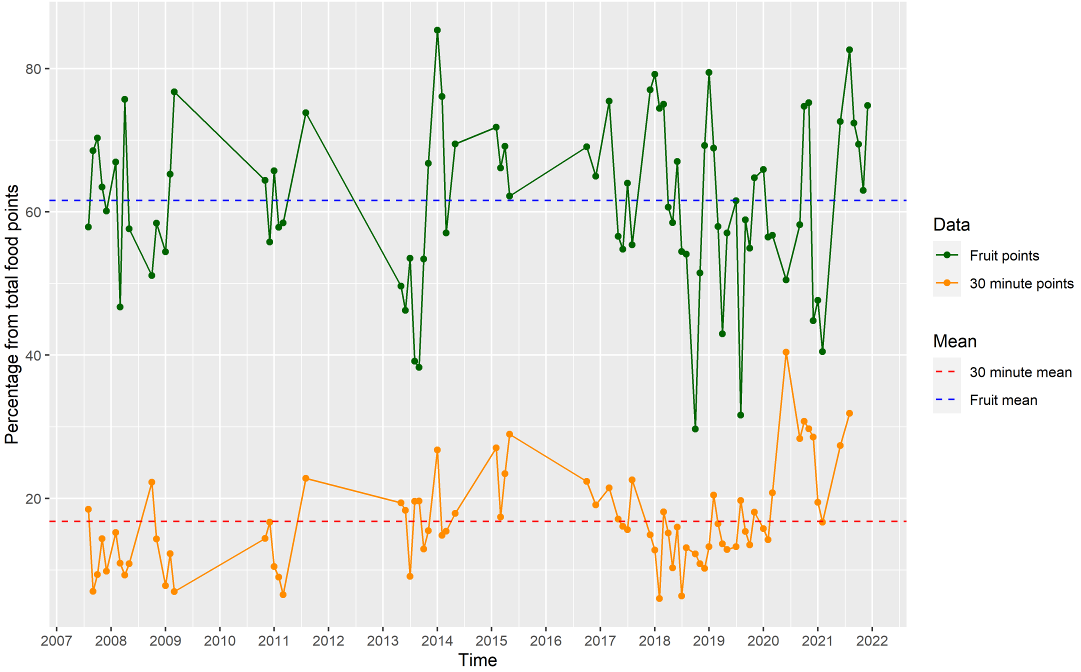


FIGURE 3.4: Percentage of fruit consumed out of all food during focal follows from 2007 to 2021. A minimum number of 10 follows per month was required. For each investigated month, the percentage of fruit (in green) and 30-minute points (in orange) is given. Mean values are indicated in a dashed blue and red line.

In terms of the different food types, the malacca fruit (*mlk*) was consumed the most, followed by termites (*rayap*), the liana akar susu kambing (*ask*), and other fruit (*pwn, spg, cmg, ubr, and tpsbt*). Also found in the top 10 are young leaves of the resak payo tree (*rskp*) and ants (*semut*) (Figure B.8). The main diet of orangutans consists of fruit. The rest of the food is mainly insects, for example, termites and ants and other non-fruit items, such as young leaves, vegetative matter, mature leaves, flowers, bark, vegetative matter inside a stem, and unknown food types. Regarding consumed food items, orangutans from different age-sex classes had similar behavior, except for adult females (Figure 3.5). They fed less on fruit and mature leaves but more often on young leave and vegetative matter than orangutans of the other age-sex classes.

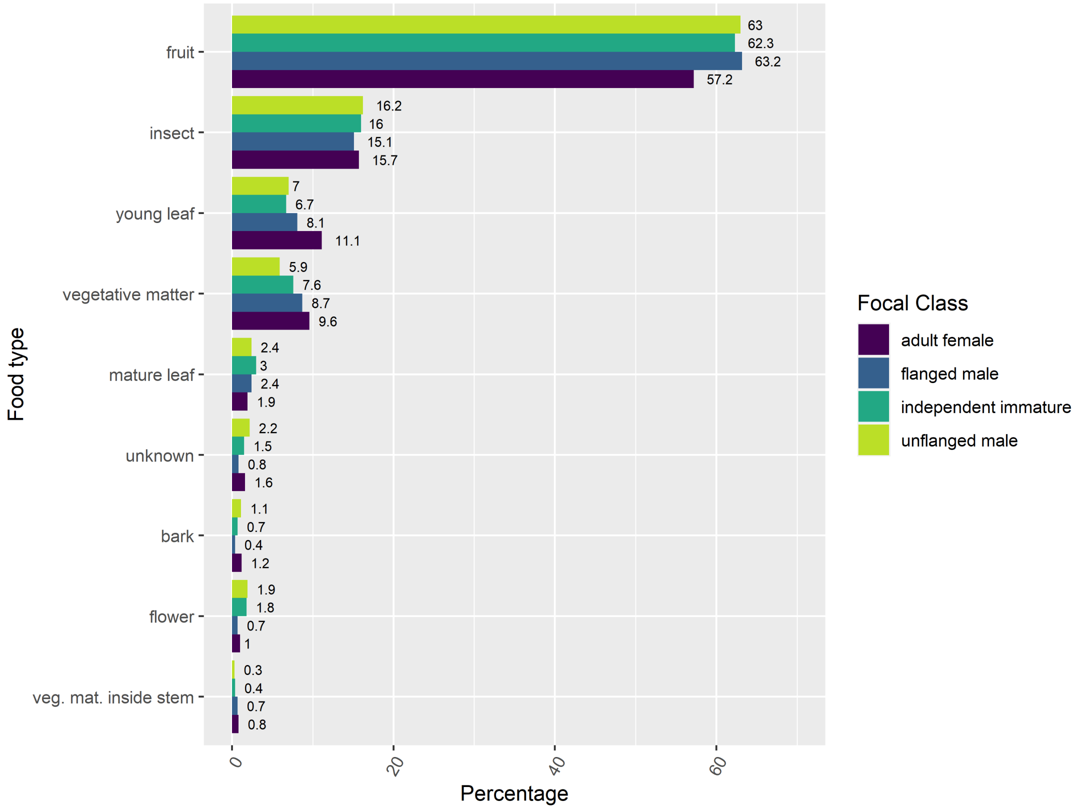


FIGURE 3.5: Food types and their percentages as part of the orangutan diet in Suaq separated for each age-sex class. Percentages are written beside each bar.

3.2.5 Food availability in Suaq

hFAI

The average hFAI value for the 80 months used in the analysis was 10.64 ±3.05. However, no information on the hFAI was available for three of those months. The availability of fruit in Suaq fluctuated between a minimum of 3.82% in March 2008 to a maximum of 17.40% of trees bearing fruit in August 2014, which implies a considerable variation in fruit availability, but no absolute scarcity of fruit. I observed no significant difference for particular months, even though there is a variation for different times throughout a year (Figure B.9). An analysis of variance (ANOVA) suggests that there is no difference in hFAI values between months (F(1) = 1.247, p = 0.268).

eFAI

Regarding the eFAI, an average monthly value of 0.84 ±0.17 was retrieved. Calculated values ranged from 0.44 in October 2021 to 1.23 in December 2007. Furthermore, for eFAI values no difference between months was found (ANOVA, F(1) = 0.618, p = 0.434) (Figure B.10). However, looking at eFAI values on a yearly basis, there is a significant difference between the years (ANOVA, F(1) = 8.741, p = 0.004). A pairwise t-test with corrections for multiple testing shows significant differences, mainly for 2011 and 2021. I noticed high eFAI values for 2011 and low eFAI values for 2021 (Figure B.11).

Comparison of hFAI with eFAI and versions of eFAI

To investigate a potential correlation between eFAI and hFAI, I performed a parametric correlation test, whereby only months with a minimum of 10 follows were included. A significant negative correlation between eFAI and hFAI was observed (Linear regression, R = - 0.29, p = 0.01) (Figure 3.6). If the analysis is performed for all 140 months without a threshold of a minimum number of follows, results suggest that this trend is decreasing but stays significant (Linear regression, R = - 0.2, p = 0.021) (Figure B.12).

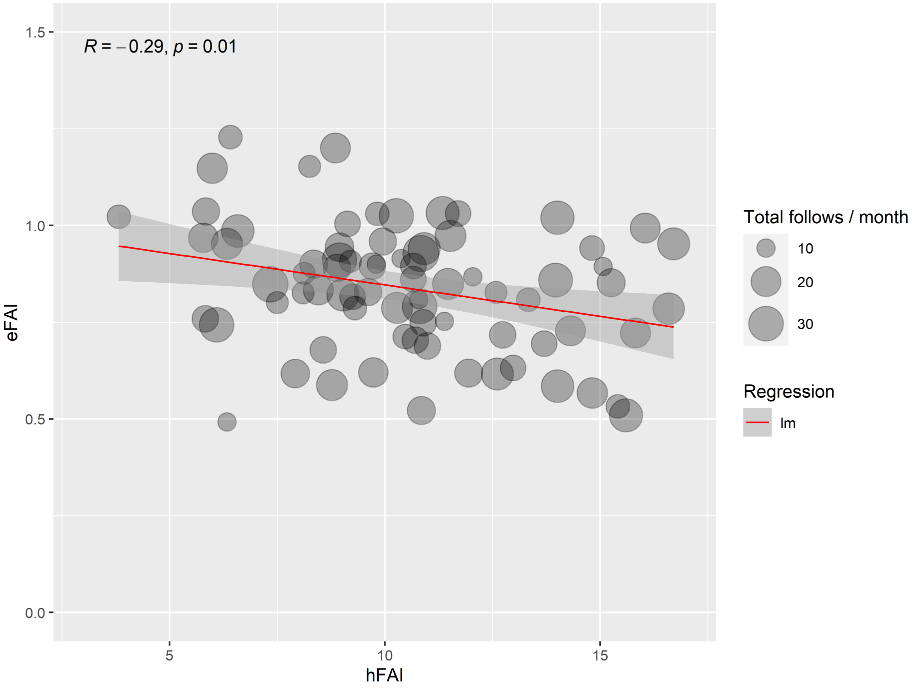


FIGURE 3.6: Comparison of eFAI and hFAI values for those months with a minimum of 10 follows. The size of the points is scaled to their included follows per month. The linear regression is drawn in red.

As the proposed eFAI considers all the food points that represent a feeding place of orangutans, whereas the hFAI only gives information on the availability of fruit in the habitat, it is suitable to compare both data for fruit only. Therefore, I trimmed the eFAI to a ratio of fruit points to range points (the so-called *fruit eFAI*). I discovered no correlation between the hFAI and this fruit eFAI values, even though when plotting the data, a negative trend is visible (Linear regression, R = - 0.17, p = 0.133) (Figure 3.7). Furthermore, when only food places with a minimum feeding time of 30 minutes are included in the calculation of the eFAI values, a slightly positive trend but no correlation of this *30-minute eFAI* with hFAI is visible across the different months (Linear regression, R = 0.096, p = 0.42) (Figure B.13).

Comparison of the versions fruit eFAI and non-fruit eFAI

For the months with a minimum of 10 follows, I observed a negative trend between the sub-indices fruit eFAI and non-fruit eFAI, but no significant correlation (Linear regression, R = - 0.1, p = 0.369) (Figure 3.8).

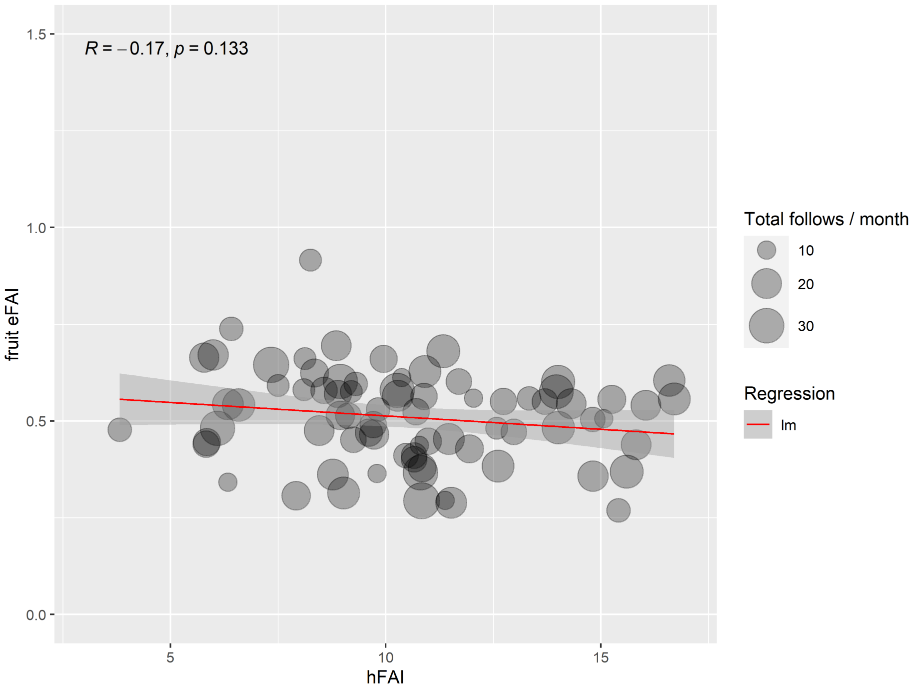


FIGURE 3.7: Comparison of fruit eFAI and hFAI values for those months with a minimum of 10 follows. The size of the points is scaled to their included follows per month. The linear regression is drawn in red.

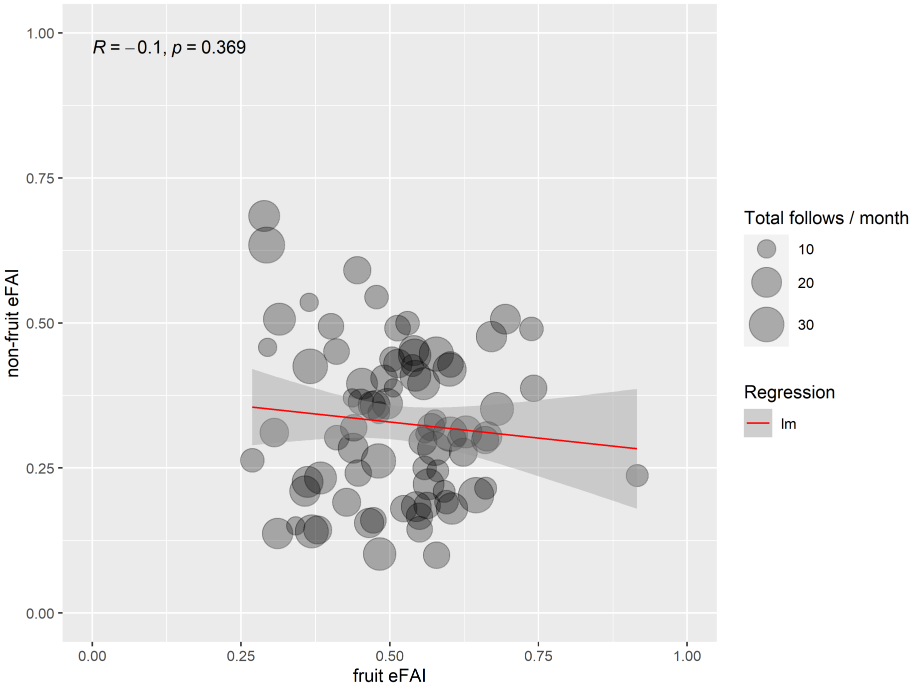


FIGURE 3.8: Comparison of fruit eFAI and non-fruit eFAI values for those months with a minimum of 10 follows. The size of the points is scaled to their included follows per month. The linear regression is drawn in red.

3.2.6 Differences in eFAI and eFAI versions for age-sex classes

I calculated an eFAI value from all follows during a month respectively and then assigned this value to those follows. Age-sex class differences can occur depending on which individuals were followed in what month. I analyzed this separately. Generally, I observed the lowest eFAI values for flanged males, followed by the eFAI values for adult females and unflanged males. At the same time, I found the highest eFAI values for independent immatures. Results show a significant difference for the age-sex classes in monthly eFAI values (Kruskal-Wallis, df = 3, χ^2 = 34.108, p < 0.001). Only between adult females and unflanged males, no significant difference was found with a pairwise Wilcoxon signed-rank test (WSR), whereas all other combinations are statistically significant (Figure 3.9). Additionally, there is a significant overall difference between males and females (WSR, p < 0.001)

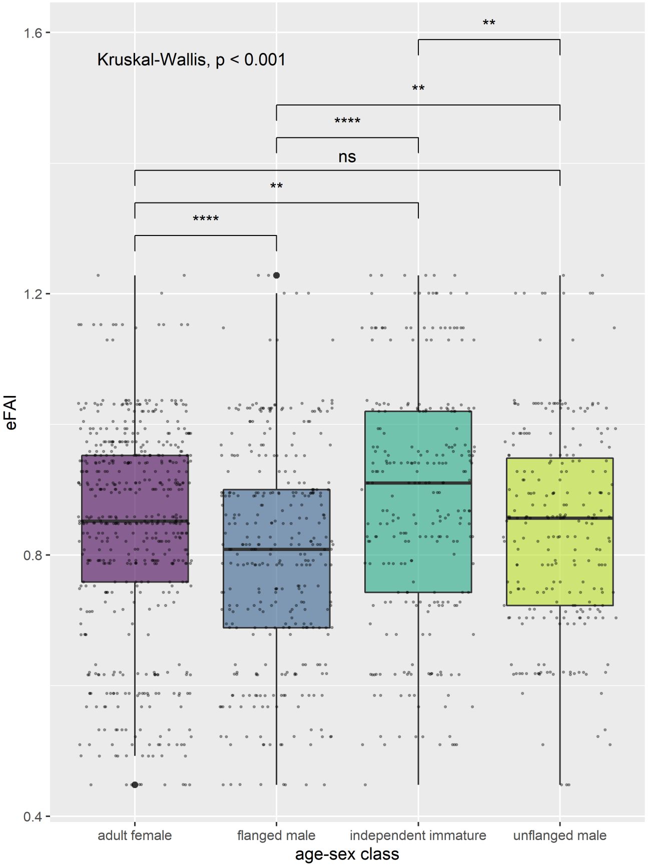


FIGURE 3.9: eFAI values for different age-sex classes. Pairwise Wilcoxon signed rank (WSR) tests and overall a Kruskal-Wallis test were performed. Significance levels: $^{****}p < 0.0001$; $^{**}p < 0.01$; ns $p > 0.05$

Further analysis for age-sex classes showed differences in the fruit eFAI (Kruskal-Wallis, df = 3, χ^2 = 28.327, p < 0.001) and non-fruit eFAI (Kruskal-Wallis, df = 3, χ^2 = 20.673, p < 0.001). For fruit eFAI, I detected a significant difference between all age-sex classes except for the comparison of adult females to flanged males. Independent immatures indicated higher values for the fruit eFAI per month, whereas unflanged males showed the least variation in the data (Figure B.14). I found the highest non-fruit eFAI values for independent immatures and the lowest for flanged males (Figure B.15).

The 30-minute eFAI also showed significant differences between the age-sex classes (Kruskal-Wallis, df = 3, χ^2 = 35.006, $p < 0.001$). Values were significantly higher for flanged males compared to all other age-sex classes, whereas no other pairings indicated significant variations between each other (Figure B.16).

3.2.7 eFAI variations in a hexagonal grid

The spatial distribution of all feeding locations in relation to the range points indicates that over the whole research period, there are differences in how many trees are available or frequented in which subarea of the study site. The calculated eFAI in the cells demonstrates the same trends as seen for the Pearson residuals in Section 3.2.1. eFAI values tend to be higher in the center, the South, and North of the research area but lower in the East, Southeast, and along the river (Figure 3.10). These trends also hold for a grid cell size of 1000 meters.

The analysis of the eFAI values has shown that in some research periods in the cells along the drawn border of the research area, no follows were conducted and, therefore, no eFAI was calculated (Figure B.17). For the center of the area and along the river, eFAI values are available for all research periods. Trends in those values indicate usually higher eFAI in the center (0.49 - 2.4) and lower ones along the river (0.33 - 1).

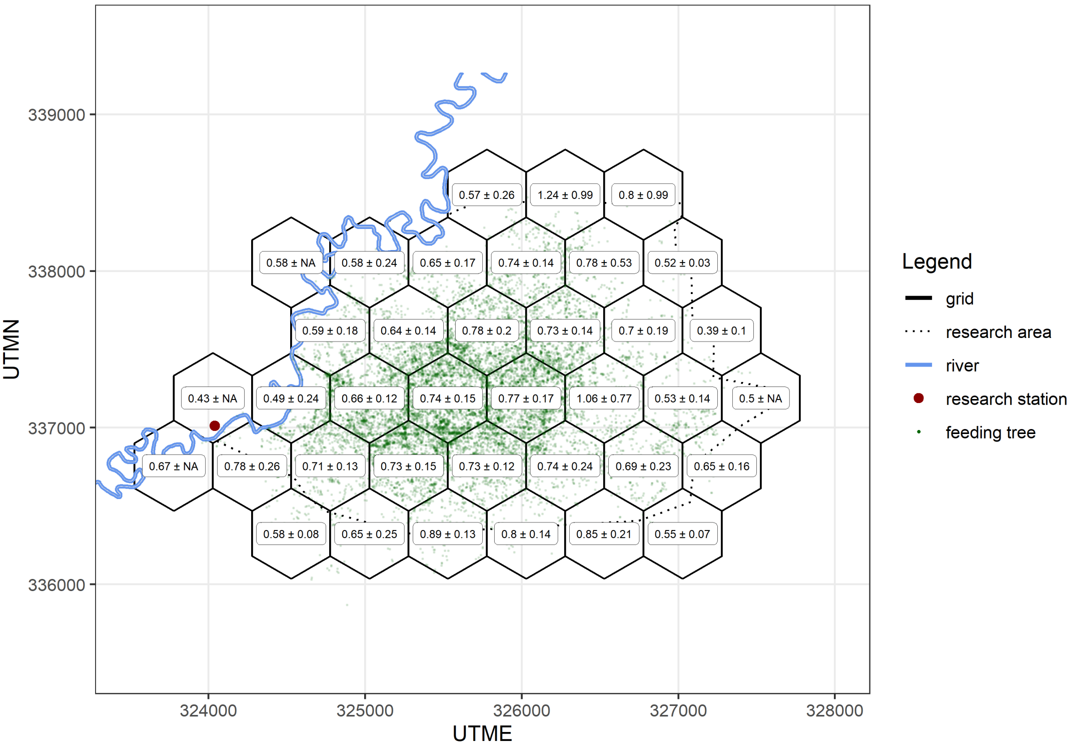


FIGURE 3.10: Mean eFAI values and standard deviations in hexagonal grid cells of 500 m for research periods of three years, respectively. NA values occur if the specific cell only contains information from one research period. Then, it was not possible to calculate standard deviations.

I discovered different trends for the two versions fruit eFAI and non-fruit eFAI. For mean fruit eFAI in the grid cells, a similar trend in higher and lower values compared to the mean eFAI values can be observed (Figure B.18). However, the non-fruit eFAI indicates a more even distribution in the mean values with no great difference between the center, the North, the South, and the grid cells along the river, except for outlier values along the border of the research area, where not many data points were taken (Figure B.19).

3.3 Discussion

3.3.1 Allocation of feeding points

Generally, I conclude that the automated process of validating and allocating feeding points from the behavioral data to the manually set feeding tree points in the field (**RQ A.1**) was suitable. Thereby, I found many new feeding points longer than 5 minutes (Section 3.2.3), which were essential for the calculation of the new eFAI (Section 3.2.5) and the different versions thereof. No previous findings for such an approach exist with this data in Suaq, a comparison to a baseline is therefore not possible.

As for the question, if the process of manually collecting feeding tree locations in the *waypoint GPS data* could be replaced, I would reject my hypothesis that an automated process for allocating feeding tree locations from the *behavioral data* could do so (**RQ A.1**). First of all, researchers are reporting behavioral information in both data sets. However, the time intervals and purposes are very different. In the *behavioral data*, orangutan behavior in two-minute steps is listed, but in less detail. In contrast, in the *waypoint GPS data* coordinates are taken every 30 minutes, and more special behavior is noted (e.g., feeding points longer than 5 minutes, experiments, or long calls). This impression on-site is needed for a good understanding of orangutan behavior.

Secondly, for some follows, the *behavioral data* is not complete for the following time or not at all available. Incompletion makes comparison impossible and introduces uncertainty. If for specific follows during a month, the *behavioral data* is missing, no or fewer additional feeding points are added compared to other months. Missing feeding points influence the eFAI calculation. Therefore, the value for a particular month can be reduced even though it would be higher with complete data. Nevertheless, the analysis of joined feeding points showed that even though there is a considerable variation between the months, no month of the year significantly differs from the others (Section 3.2.3). On a yearly basis, the average added number of feeding points per follow varied from 1.18 to 12.93. That is a major variation. However, this variation depends on the data collection and for which follows the *behavioral data* is available. Interestingly, for 2013 to 2017, there is a tendency towards more added feeding points, whereas, for recent and prior years, fewer points were added. This could mean that the collecting process was optimized in the last few years, and fewer feeding points needed to be added.

Lastly, not all feeding points from the *behavioral data* could be matched with their counterparts in the *waypoint GPS data*. Some feeding points remained that are only found in the *waypoint GPS data*. They were also included in the calculation of the eFAI. This information would be lost if only the behavioral feeding points were used. Therefore, in my opinion, and from the insights into both data sets, neither one can replace the other. Instead, the information from the *behavioral data* can undoubtedly be used to improve and complement the *waypoint GPS data* to obtain as much accurate information as possible. Additionally, the inspection of a correct number of range points in Section 2.3 was as essential for an adequate eFAI calculation as the allocation process.

A comparison of the locations of the coordinates of the *waypoint GPS data* and *behavioral data* showed that they are mostly very close to each other. In this thesis, I could confirm that these measurements of the same feeding points are accurate with an average deviation of around 11 m and within the range of a general GPS error of lower than 10 m (Section 2.5). This GPS distance deviation is in line with the accuracy analysis of Wartmann (2008), where a mean positioning error of 9.8 m was found for the research site in Tuanan. Ashbury (2020) found two main reasons for GPS errors in the rain forest. First, when orangutans would feed or rest in one place for a longer time, multiple 30-minute range points would lead to deviating locations from actually the same place. The reason for this is primarily low satellite reception causing a GPS inaccuracy or observers moving around to find appropriate observation points. Second, complete satellite loss caused so-called 'jitter' in the GPS points resulting in outlier values. Due to the validation of the GPS points by comparing them against each other and finding outliers manually in the cleaning process, I renounced further processing of the *waypoint GPS data* and the combination of the *behavioral and track GPS data*. Confirming a good accuracy helps to obtain appropriate estimates of movement parameters, for example, DJL or sinuosity of movement in Chapter 4. It is further useful to know for the researchers that they are setting the GPS points accurately because they need to wait in the field until the orangutans have left and try to find the exact spot on the rain forest ground in order not to disturb the focal (Section 2.2).

Visual inspection of calculated eFAI values per month, with and without the allocated feeding points, confirms that the automatic process is an improvement for eFAI calculation and the completeness of the data (Figure B.7). For many months in 2013, 2015, and 2017 almost no feeding points were recorded in the field (Subfigure A), which led to an underestimation of the calculated eFAI. On the contrary, the local spike at the end of 2010 and the beginning of 2011 was influenced by higher temporal resolution in some follows, leading to excessive feeding points and an overestimation of the eFAI. Those follows were filtered manually and led to a decrease in the local spike (B). Furthermore, the clumps in 2013, 2017, and 2019 in (A), where several consecutive months have almost the same eFAI, changed to a variation in values ranging between around 0.5 and 1.0 in (B). This limitation in the range of eFAI values is not so astonishing, as the Suaq orangutans were expected to have food year-round in their habitat (Morrogh-Bernard et al., 2009). At Suaq, the amount of time the orangutans spend feeding does not change as much as in other places (for example, in Tuanan on Borneo) because the orangutans are not restricted by a scarcity of fruit (Marshall et al., 2009a; Morrogh-Bernard et al., 2009).

3.3.2 What and how long do the orangutans at Suaq eat?

Fruit are considered high-quality items in the diet of orangutans (Marshall et al., 2009a), but insects, vegetative matter, and leaves are an essential part of their diet too. In Section 3.2.4, I showed that the percentage of fruit points out of all feeding points varies between 30% and 90% and, on average, is around 62%. This number is in line with a study by Vogel et al. (2017) where they found that around 60% non-fig fruit was consumed in Tuanan. In contrast, a comparable study for many research sites found a much lower value of 34% for consumed fruit in Suaq compared to all other study sites (Russon et al., 2009). For Ketambe on Sumatra Wich et al. (2006) found that 67.5% of the diet were fruit, which is quite similar to the value found in this thesis. In contrast to the study by Russon et al. (2009) for data from Suaq, more leaves were consumed in the period analyzed by me. Overall, the orangutan diet in Suaq represented as a percentage of the feeding points is similar to what is listed by Morrogh-Bernard et al. (2009) as a percentage of total feeding time (66.2% for fruit, 15.5% for leaves, 13.4% for invertebrates, 1.1% for bark and 3.8% for other food items).

In terms of consumed food items, I could show that orangutans from different age-sex classes have similar diet compositions, except for adult females (Figure 3.5). They fed at fewer feeding locations on fruit and mature leaves but at more places on young leaves and vegetative matter than orangutans from all other age-sex classes. Female orangutans need to maintain lactation and pregnancy (Schuppli et al., 2016a) by consuming specific nutrient- and protein-rich food found, for example, in young leaves (Vogel et al., 2017). This behavior is in line with findings from Schuppli et al. (2021) for Bornean orangutans. They found that adult females have significantly more complex diets from a broader spectrum than males. Additionally, adult females, especially mothers, play an active role in the skill acquisition of their offspring (Mikeliban et al., 2021). Furthermore, mothers are the primary role models for immature orangutans in terms of social learning (Schuppli et al., 2016b). Therefore, consuming a broad diet may allow their offspring to learn about these items.

Wich et al. (2006) showed that the orangutan diet on Sumatra is little influenced by fruit availability fluctuations. Consequently, when on average only a part of the energy intake comes from fruit, the hFAI measure for fruit found in the habitat is an incomplete measure of overall food availability. First, the index only looks at fruit availability in the habitat but to quantify food availability all food types need to be taken into account. For example, a plant item can be recorded as food at one study site and not at another due to ranked preferences of orangutans, even though this plant item is available at both (Marshall et al., 2009a). Second, not all of the fruit found in the habitat is consumed. Therefore, the aim of **RQ A.2** was to assess a possible alternative measure of food availability that takes into account all food types that are indeed eaten by the orangutans and the time spent feeding different plant items.

Such an alternative measure of food availability could even be more helpful at other sites, such as Tuanan, where the fruit fluctuation between seasons is much higher than in Suaq, which was shown for low, medium, and high fruiting periods, for example, by Vogel et al. (2017). In Tuanan, Vogel et al. (2017) found that overall there was no relation between protein intake and fruit availability because orangutans include a constant amount of protein across all seasons in their diet. Thus, they do not only rely on young leaves that are higher in protein (Vogel et al., 2017). However, on an age-sex class level, they showed a negative correlation between protein intake and hFAI for adult females and unflanged males. Further, Harrison et al. (2010) mentioned that (habitat) fruit availability may not always be an accurate indicator of energy intake. Nevertheless, also the introduced eFAI does not indicate the caloric value of the consumed food, which would be necessary for calculating a suitable energy balance as suggested by Knott (2005).

Lastly, the 30-minute feeding points indicate whether more food is consumed at a specific location. Because orangutans spend more time there, these feeding locations are assumed to have a greater influence on the animals, and their energy intake is higher than their Total Energy Expenditure (TEE) at these places (Pontzer, 2017). In my analysis, an average of around 17% of all feeding points are longer than 30 minutes (Figure 3.4). The variation of 30-min feeding points for different months may also be explained by the consumption of an increased amount of fruit in general. Knott (2005) suggested that when fruit is abundant, orangutans generally increase their feeding time, whereas other primates do not follow this pattern. The reason seems to be that they can put on fat reserves when profiting from high fruit abundance (Knott, 2005). However, in the results here, no correlation was found between the percentages in fruit consumption and 30-minute feeding location (Section 3.2.4). Nevertheless, caution is required in interpreting the results in Figure 3.4 as the information on the feeding duration is stemming only from the allocated *behavioral data* (Section 2.3) and cannot be validated by the initial *waypoint GPS data*.

3.3.3 Influence of bootstrapping on the number of focal follows needed

For the analysis in Chapter 4 and the interpretation of the results in Chapter 3, it is helpful to know the dispersion of the data in the new index. The second part of **RQ A.2** focused on reliably assessing the eFAI and finding a robust and representative value for this index. Individual orangutans and orangutans of different age-sex classes differ in their feeding behavior and energy intake (Harrison et al., 2010; Vogel et al., 2017). Furthermore, the feeding behavior of an individual can vary across follow days. This limitation could influence the monthly eFAI when the feeding points during a month stem only from one particular individual or day. Therefore, a larger number of follows from a larger number of focal individuals included in the calculation of eFAI increases the likelihood that the eFAI is independent of one focal and its feeding preferences and that the value reliably mirrors the experienced food availability. As the number of follows strongly influences the monthly data, it was a good indicator for a test with the bootstrapping resampling method, where follows were randomly selected. The expectation was that around 5 to 10 follows would be required to achieve a proper stabilization of the mean values and thus robustness of the new index (**RQ A.2**).

In Figure B.6, I show a right-skewed distribution meaning that most of the months need less than 10 follows to express a lower variation in the data and mean values, respectively. An average of 8.19 follows as a minimum per month was found. However, some months need up to 15 follows with some outliers of up to 32. I based the decision for a minimum number of 10 follows on an appropriate balance between the independence of the data and the loss of too much data. By including the bootstrapping resampling in the work process, I omitted 60 months because they had less than 10 follows, which can be seen in Figure B.7 (C). A more conservative cutoff value of 15 follows per month would have been suitable from the perspective of increased estimation robustness but was rejected because another 29 of the remaining 80 months of data would have been omitted.

Furthermore, a cutoff size of 10 follows per month is probably large enough to have at least 2 or 3 individuals, at best from different age-sex classes, influencing the monthly eFAI. This happens because one focal is seldom followed for more than a few days consecutively, and observers are restricted to ten days to minimize the disturbances on the orangutan (Schuppli, personal communication, 2022).

I calculated the coefficient of variation (CV) from the proportion of the standard deviation to the mean for each month and each sample size of the bootstrapping method. One hundred bootstrap replications per sample size, where follows were picked randomly with replacement, are usually informative and give a reasonable estimate (Efron and Tibshirani, 1993), in my case here, for eFAI values. A lower CV generally indicates higher reliability in the bootstrap replications. Confidence intervals were not chosen as a decision criterion, as they are calculated partly based on the standard deviation and the mean besides a score for the 95% confidence interval and a value for the sample size. Average values for a minimum number of follows per month based on thresholds of 5% and 20% for the CV showed that 10% is an appropriate cutoff (Section 3.2.2).

3.3.4 Food availability in space and time

On the one hand, **RQ A.3** focused on the variation of hFAI with time. In Suaq, monthly changes in hFAI can be observed, with between 4 and 17% of trees bearing fruit (Section 3.2.5). Missing clear seasons of fruiting in the region makes it harder to capture temporal patterns of fruit availability variation. However, hFAI values indicate that the Sumatran orangutans at Suaq do not face any fruit scarcity and probably explain why there is less variation in the time spent feeding on fruit in Suaq than in other study areas, for example, Tuanan or Gunung Palung (Morrogh-Bernard et al., 2009). Low fruit availability is, for example, referred to as below a threshold of 3% (Vogel et al., 2017) or 4.46% (Ashbury et al., 2022) in Tuanan on Borneo. Even though certain months during the year seem to have a lower, such as in March, or higher mean value, such as in June, I found no significant difference between the months (Figure B.9). This result is in line with the analysis of Graf (2021) for the study period from 2010 to 2020.

On the other hand, **RQ A.3** assessed the variation of food availability with space and time. For eFAI, no significant difference between the months was found (Figure B.10). However, an analysis on a yearly basis showed significant differences for the years 2011 and 2021 (Figure B.11). This trend could have several reasons. On the one hand, for these two years, more or fewer *feeding points per follow* could have been added, respectively, which would have influenced the eFAI calculation. The year 2021 indeed has a low number of feeding points per follow added (1.18), whereas for the year 2011 no unusually high added number was found (5.31) (Section 3.2.3). For the year 2021, this could explain the low eFAI, even though it could simply show that newer data from 2021 would not need much data to be added because it is already very complete regarding the feeding points. The year 2011, on the other hand, was already found to be different from other years and to have lower fruit availability in Graf (2021). As the relationship between hFAI and eFAI was found to be negative (Section 3.2.5), higher eFAI values for this year could be possible, suggesting a period where overall more food was consumed.

Interestingly, the calculated monthly eFAI values differ if analyzed for age-sex classes (Figure 3.9). All pairwise comparisons except for adult females and unflanged males were significant. These trends show that it is important to analyze the data in Chapter 4 for different age-sex classes. Still, the results have to be interpreted with caution. If there is large individual variation, individuals over-represented in the sample could bias the results.

Nevertheless, a possible reason for significant differences in eFAI values might be different foraging strategies between age-sex classes represented in the experienced food availability. Vogel et al. (2017) have shown that energy intake varies between age-sex classes, with flanged males having the lowest and independent immatures (females and males) having the highest intake. However, Harrison et al. (2010) mentioned in a study in the nonmasting Sabangau peat-swamp forest on Borneo a positive relationship between daily energy intake and fruit availability for flanged males, but not for adult females or unflanged males, which they interpreted as possible differences in foraging strategies. Therefore, habitat fruit availability might not always be an appropriate indicator of energy intake or balance (Harrison et al., 2010).

My results suggest a tendency to lower eFAI values for flanged males compared to the other age-sex classes. They are found at fewer feeding spots during the follows, whereas independent immatures are found the most. Lower eFAI values for flanged males would agree with findings from Vogel et al. (2017), where they showed lower energy intake for flanged males than for all other age-sex classes. Lower eFAI values for flanged males could suggest an 'energy conserving' strategy. Nevertheless, this does not give any information on the feeding time, available food types, or energy intake at a certain location. Therefore, I also analyzed the variations of fruit eFAI, non-fruit eFAI, and 30-minute eFAI. Flanged males have significantly higher eFAI values that are based on feeding points for more than 30 minutes than all other age-sex classes (Figure B.16), but on average lower fruit eFAI and non-fruit eFAI values (Figures B.14 and B.15). In conclusion, this means that flanged males tend to search for fewer feeding locations, but they spend, on average, more time feeding there than orangutans from other age-sex classes. This result fits with observations in the field, where flanged males often spend extended periods of time at good feeding spots (Schuppli, personal communication, 2022). This behavior suggests that for flanged males, spending extended time exploiting one resource rather than quickly switching between resources makes more sense. This may be because for flanged males movement is more costly than for the other age-sex classes because of their big body size. Compared to other age-sex classes, a reduced movement also coincides with the idea that they do not need to actively roam through the area in search of fertile females compared to unflanged males (Dunkel et al., 2013; Utami Atmoko et al., 2009). However, a higher 30-minute eFAI for flanged males in Suaq would be in contrast with Borneon flanged males that had the lowest feeding time of all age-sex classes (Vogel et al., 2017).

In the case of fruit eFAI values, I found no significant difference between adult females and flanged males, unlike for all other pairwise comparisons (Figure B.14). Independent immatures are found on average the most at fruit and non-fruit locations (Figures B.14 and B.15). However, they do not differ from adult females and unflanged males regarding their 30-minute feeding points. Accordingly, independent immatures spend their day searching for many (fruit) trees, where they spend less time feeding. This behavior shows how important high-calorie food is for them to ensure sufficient energy intake and to support their growing bodies (Vogel et al., 2017). On top of that, they are most likely less competent at locating big food patches. Thus, they end up switching between food patches faster than other individuals (Schuppli et al., 2016a).

For adult females, I could already show that the diet composition differed from all other age-sex classes (see above). Additionally, adult females have a low 30-minute eFAI (Figure B.16) which is in line with the hypothesis that they need a balanced diet from different food items found at various feeding places to get the proper nutrients for pregnancy and lactation (Noordwijk et al., 2013; Schuppli et al., 2016a).

3.3.5 Comparison of hFAI with eFAI and versions of eFAI

One question in **RQ A.3** explored the relationship between hFAI and eFAI. In the analysis, both indices were compared to each other (Section 3.2.5). Results showed for all considered months (R = - 0.2, p = 0.021) and for those with a minimum of 10 follows (R = - 0.29, p = 0.0097) a significant negative correlation (Figures B.12 and 3.6). On the contrary, I expected a positive correlation to some degree, as the orangutans can only experience the food that is actually available in the habitat. Both indices try to give information on the food or fruit quantity in the study area, and it seems reasonable that they are somehow associated. However, the negative relationship might indicate that food is consumed at fewer locations with more fruit available in the habitat. This relation would fit with maintaining the energy budget because orangutans do not need to feed at many different places when facing high fruit abundance in the habitat. It would also mean that the hFAI lacks in explaining which food from the habitat plays a role in the diet of orangutans and that the index would not be representative of the research area regarding food availability.

However, when comparing eFAI to hFAI, I compared all feeding points to the percentage of fruit-bearing trees in the habitat. Therefore, I compared fruit eFAI (including fruit feeding points only) and hFAI (**RQ A.4**). I discovered no significant correlation, even though there is a negative trend (Figure 3.7). Consequently, if no connection is found, it means that experienced fruit availability is not mainly driven by the availability of fruit in the habitat. This would mean that no matter how many trees bear fruit, orangutans search for and consume them as they are their favored food items (Knott, 2005). Again, this may be explained by the fact that there is always plentiful fruit to find and no scarcity is faced (Morrogh-Bernard et al., 2009). Nevertheless, a slightly negative trend might suggest that if orangutans encounter more fruit in their habitat, they are likely to eat less fruit during a follow, which also means they can spend more energy and time on other activities and bother less searching for high-calorie food. Additionally, I compared the sub-indices fruit eFAI and non-fruit eFAI with each other, but I found no significant correlation (Figure 3.8). However, the negative trend between the two sub-indices could indicate that when orangutans experience less fruit, they compensate by eating more non-fruit items.

Lastly, I found no correlation between the 30-minute eFAI and the hFAI (Figure B.13). The distribution of the monthly points suggests that longer feeding times do not depend on fruit availability in the habitat (**RQ A.4**). In comparison, Vogel et al. (2017) have described a negative relationship between total feeding time and habitat FAI. Nevertheless, this thesis showed that for the analyzed data, percentages of 30-minute points and fruit points do not correlate with each other (Section 3.2.4).

3.3.6 Food locations in Suaq and eFAI values in grid cells

One last research goal in this first part of the thesis was to explore the spatial variation of the food availability (**RQ A.3**). Both, eFAI (Section 3.2.7) and Pearson residuals from the observed versus the expected food locations (Section 3.2.1) have shown trends in the research area for grid cells of 500 meters (Figures B.2 and B.17). Over the whole study period, mean eFAI values are higher in the center, the South, and the North but slightly lower in the East and along the Krueng Lembang river in the West of the research area. For the fruit eFAI values I observed the same trends (Figure B.18). One reason could be the layout of the area as a whole, featuring different main habitat types described in Singleton and Schaik (2001) and Van Schaik (1999). Patterns of fruit availability vary strongly between forest types on Borneo (Cannon et al., 2007). Soil types, besides other factors, influence the growth of different vegetation. Therefore, differing habitats are more likely (in peat swamps and regularly flooded backswamps on muddy soils) or less likely (in adjacent hills to the East or the tall riverine forest along the river) to include fruit that the orangutans consume. A comparable study by Marshall et al. (2009a) found differences in fruit availability for three forest types (peat, dry, and riverine) in Suaq. Non-fruit vegetation (e.g. insects, lianas, or leaves), on the other hand, can be found throughout the whole research area. That is probably why there is not a great difference in mean non-fruit eFAI values between the center, the North, the South, and the grid cells along the river (Figure B.19).

Other reasons for the discovered differences throughout the study area might be the grid cell size, of which I tested only 500 and 1000 meters, the concept of grid cells with an arbitrary origin, the corresponding sample sizes, or the concept of three-year research periods. Even though the data was summed for three years respectively, I could not calculate an eFAI value for all grid cells in the research area. The restriction resulted in small standard deviations or NA values if data was available only for one period (Figure 3.10). Further, results show higher numbers of the eFAI along the edges of the research area (Figure B.17). These unrealistically high eFAI values stem from only very few data points in the corresponding cells and are thus likely an edge effect. An eFAI value of three in the research period of 2013 to 2015 in a Northern cell resulted, for example, from only three feeding locations compared to one range point. The same factors could have influenced the fruit eFAI and non-fruit eFAI in the grid cells. Therefore, eFAI, fruit eFAI, and non-fruit eFAI values based on a small amount of data need to be handled with care.

Analyzing eFAI values in grid cells in five research periods of three years shows local spatial variances that could not be captured before by relying on one specific hFAI value. Unfortunately, a more detailed spatial and temporal analysis on a monthly basis was not possible due to the lack of sufficient data in the form of focal follows. Therefore, I only conducted the following analysis in Chapter 4 for the temporal variation in eFAI values on a monthly basis.

Chapter 4

Movement analysis

4.1 Methodology

4.1.1 Movement parameters

Many indicators are used within the field of movement ecology to analyze where, when and why individuals move in their varying natural environments (Demšar et al., 2015; Nathan et al., 2008). Dodge et al. (2008) and Seidel et al. (2018) feature an overview of commonly used path or movement metrics. Turning angle and step length belong to the category of primary metrics that are computed directly from each step-wise relocation. Therefore, they are influenced by the spatial and temporal resolution of the data collection, which makes a fixed sampling rate more convenient (Calenge et al., 2009; Codling and Hill, 2005). On the other hand, secondary metrics can be derived from primary metrics and represent summary statistics, for example, total displacement distance, straightness index, or tortuosity, here specified as the sinuosity index (Seidel et al., 2018).

Day journey length

The Day Journey Length (DJL) or total daily travel distance is one of the main indicators that can be derived from animal movement data to gain ecological information about the behavior, energetics, and demography (Rowcliffe et al., 2012). Differences in DJL are frequently interpreted as a sign of changes in foraging strategies (Campbell-Smith et al., 2011; Vogel et al., 2017; Wich et al., 2009) and could allow the inference of energy expenditure in orangutans (Knott et al., 2009).

DJL is derived from the step length represented in the Euclidean distance between consecutive GPS points. Subsequently, those distances are then summed up for a defined time. Daily distances were previously calculated for Suaq, for example, in Ashbury et al. (2020). Here, the period spans from the morning to the night nest, representing the diurnal behavior of an orangutan and a nest-to-nest (NN) follow day. However, this representation of an animal movement is only an approximation as the actual traveled distance is unknown when the location is not tracked constantly (e.g., by means of a tracker). DJL further depends on the sampling interval of the data collection.

Total displacement and tortuosity of movement

The Total Displacement Distance (TDD) is also called the nest-to-nest distance, as it is referred to as the straight-line distance from the start to the end point of a path, for orangutans usually the morning and night nest. Other ecological studies frequently apply this idea to distinguish between migratory and territorial behavior, typically by categorizing several migration stages using the total distance between each GPS point and the start location. This distance is referred to as the Net Squared Displacement (NSD) (Bunnefeld et al., 2011; Calenge et al., 2009; Seidel et al., 2018). The TDD for each follow is then calculated from the NSD by taking its root. However, TDD is not so important in this thesis, as it is more used to calculate the straightness of orangutan movements.

Besides analyzing DJLs and TDDs of animals, other metrics have been developed to focus more on, and describe, turns in the movement trajectories. A crucial factor in searching behaviors and movement efficiency is the tortuosity of an animal's path (Benhamou, 2004). It has been used as a parameter to reflect how intense the search for food by an animal is (Calenge et al., 2009). The Straightness Index (SI) and the tortuosity, also called the sinuosity index, are metrics that assess how much movement trajectories deviate from straight lines (Seidel et al., 2018).

The SI is computed by dividing the TDD by the DJL from the morning to the night nest (Equation 4.1), where resulting values near 0 mean highly tortuous and near 1 represent very straight movements, corresponding to a more oriented path (Batschelet, 1981; Benhamou, 2004). Benhamou (2004) showed that SI reliably estimates the efficiency of an oriented path. However, SI can not be applied to random search paths because the index decreases when the total movement increases, tending towards zero for an infinitely long path (Almeida et al., 2010).

Schuppli et al. (2016a) used the inverse straightness index, which in their paper is referred to as the ramble ratio (DJL divided by TDD), to assess differences in movement between age classes of orangutans in Suaq on Sumatra and Tuanan on Borneo. They hypothesized that orangutan individuals that know the spatiotemporal resource availability in their habitat less well (i.e., independent immatures) would have higher ramble ratios meaning highly tortuous movements. However, they discovered no difference between independent immatures and adults but a significant difference in ramble ratio between the two study sites with more direct travel routes for Tuanan individuals (Schuppli et al., 2016a).

On the contrary, the sinuosity index is a metric that includes average step lengths and turning angles (Equation 4.2). It is applicable for a random search path, where each step is correlated to the previous one (Almeida et al., 2010; Benhamou, 2004). This index gives values between 0, which denotes a straight line, and 1, corresponding to a highly tortuous movement. However, this sinuosity measure is scale-dependent, which means that the same animal trajectories result in different sinuosity values if analyzed on varying scales (Almeida et al., 2010). Moreover, trajectories are assumed to be regular because the relative angle is related to a given time scale (Calenge et al., 2009). In this thesis, I presume that the standardized nest-to-nest follows are normalized in 30-minute steps leading to comparable results between different individuals (Section 4.1.2).

$$Straightness = \frac{TDD}{DJL} \tag{4.1}$$

Simple Straightness Index (SI) by Batschelet (1981). The ramble ratio used in Schuppli et al. (2016a), however, is the inverse SI.

$$Sinuosity = 2\left[p\left(\frac{1+c}{1-c}+b^2\right)\right]^{-0.5} \tag{4.2}$$

Sinuosity Index from Benhamou (2004), Equation 8, with p = average step-length, c = mean cosine of turning angles, b = coefficient of variation (CV) of step-length.

4.1.2 Workflow

Based on the allocation process and the bootstrapping resampling in Chapter 3, the data set with a minimum number of 10 follows per month was further analyzed. I present these results in Section 4.2. Additionally, movement parameters were calculated based on the full data set, containing all NN follows of all 140 months. The corresponding model results are included in Appendix C. For the analyses, only range points, besides morning and night nest points, were used from the data set to have a standardized time lag between the GPS points, which is important in the ecological analysis of movement parameters (Calenge et al., 2009; Codling and Hill, 2005). I excluded GPS points for long calls, experiments, and other data points. For the movement analysis, I considered only nest-to-nest follows including morning and night nests as start and end points. This restriction reduced the total number of NN follows in Suaq to 648 and 770 when all months were included. However, because in certain follows no information on the corresponding hFAI value was available, the number of analyzed NN follows in the statistical analysis decreased further to 625 and 735, respectively (Figure 2.2).

For the resulting data set, I calculated trajectories for each follow and step lengths between the GPS points with the package **adehabitatLT** (version 0.3.25; Calenge, 2006). I summed up Euclidean distances to represent the DJL. The function in the **adehabitatLT** package further calculated the step-wise time lag, the NSD, and the relative turning angle between the GPS points. Taking the root of the NSD from the first to the last point in the respective follow resulted in the TDD. I computed the SI for each follow by calculating the TDD/DJL ratio (Equation 4.1). For the sinuosity index for each follow, I used the formula from the **trajr** package (version 1.4.0; McLean and Skowron Volponi, 2018) (Equation 4.2), corresponding to the original formula in Benhamou (2004).

4.1.3 Statistical analysis

For the statistical analysis, in the first step, I produced a scatterplot and Pearson's correlation coefficients (Figure C.1) to gain an overview of the movement parameter and the different variables using the **GGally** package (version 2.1.2; Schloerke et al., 2021). Before running the models, when visually assessing the relationships between the variables, I discovered that the eFAI values did not correlate with the DJL or the sinuosity index for either the whole data or if separated for sexes and age-sex classes (Figures C.2 and C.5). However, if split into the fruit eFAI and non-fruit eFAI parts, the values showed some opposing correlations with DJL and the sinuosity index on significant levels (Figures C.3 and C.6). This insight influenced the choice of the fixed effects in the models described below.

Subsequently, the effects of different food availability – represented by hFAI, fruit eFAI, and non-fruit eFAI – on the movement parameters were examined using Linear Mixed-effects Models (LMMs) from the **lme4** package (version 1.1-27.1; Bates et al., 2015). The `lmer()` function in the **lme4** package was used to fit the model via Restricted

Maximum Likelihood (REML) or Maximum Likelihood (ML). In ecology, the popularity of such models has increased in the last years (Harrison et al., 2018). By incorporating a combination of fixed and random effects of the explanatory variables, they expand on traditional linear models. The utilization of random effects is particularly beneficial, as the data often shows a lot of noise, and the response variables are influenced by unknown or other factors that are not considered in this thesis. One of the key benefits is the ability to account for these effects. Movement ecology data sets are often quite complicated because they frequently exhibit biases, clustering, and non-independence (Harrison et al., 2018). This lack of independence can be corrected by adding random effects to the models. Additionally, LMMs do not need normally distributed data. In the following paragraphs, I explain which variables, models, and model diagnostics were used in this thesis.

Variables in the linear mixed-effects models

In the LMMs, the movement parameters DJL, TDD, SI, and sinuosity (Section 4.1.1) were used as *response effects* because I wanted to test if and how the different food availability affected the ranging behavior and tortuosity of orangutan movement. *Fixed effects* were hFAI, fruit eFAI, and non-fruit eFAI, representing different (habitat and experienced) food availability, besides the age-sex class in the overall models. For all other models, I used only hFAI, fruit eFAI, and non-fruit eFAI as fixed effects. The eFAI was split into a fruit and non-fruit part because I discovered that they expressed opposing trends on movement parameters as explained above (e.g. Figures C.3 and C.6). As *random effects* the month and year of a follow and the focal name were included in the LMMs to control for pseudoreplication. For the random effect focal, for example, I had multiple data points of each individual. Therefore, I included the focal name as a random effect to avoid pseudoreplication. All fixed and random effects were chosen before running the models.

Overview of linear mixed-effects models

Initially, I introduced an interaction term between the eFAI and age-sex class to account for differences regarding food availability between the age-sex classes. I analyzed the overall models with this adjustment. However, they only showed significant differences between the age-sex classes and not the effect of the eFAI and hFAI on movement parameters. Therefore, I calculated separate models for each age-sex class and the males and females. Thus, LMMs were fitted for the overall model, for each age-sex class and both sexes separately but also for a full data set (containing all NN follows of all 140 months) and a reduced one for 80 months with a minimum number of 10 follows respectively. Table 4.1 gives an exemplary overview of the different models and their names for the response effect DJL. For models with the other response effects TDD, SI, and sinuosity, the ending changes to _TDD, _SI, and _sinuosity, respectively.

How the models were assessed

To assess the significance, I compared the fitted models to the corresponding null models containing only the random effects month-year and focal name using a Likelihood Ratio Test (LRT) in the `anova()` function. In that way, I could see if the models with fixed and random effects could explain the variance in the response effects better than a random model. The log-likelihood indicator and the Akaike Information Criterion (AIC) (Sakamoto et al., 1986) were used for model selection.

TABLE 4.1: Overview of the model names for the response effect DJL.

Data set	Class	Response effect	Name
Reduced	Overall	DJL	RO_DJL
	Males		RM_DJL
	Females		RF_DJL
	Flanged males		RFM_DJL
	Adult females		RAF_DJL
	Unflanged males		RUM_DJL
	Independent immatures		RII_DJL
Full	Overall	DJL	FO_DJL
	Males		FM_DJL
	Females		FF_DJL
	Flanged males		FFM_DJL
	Adult females		FAF_DJL
	Unflanged males		FUM_DJL
	Independent immatures		FII_DJL

I used the **lmerTest** package (version 3.1-3; Kuznetsova et al., 2017) to determine p-values using Scatterthwaite's degree of freedom method for the various fixed effects. Random effects were tested by using a random effect ANOVA (`ranova()` function in the **lmerTest** package) that deletes those one-by-one and compares the results with each other.

I calculated Intraclass Correlation Coefficients (ICC) to give information on the reliability and similarity within the groups of the random effects that are used to explain the movement parameters (Nakagawa et al., 2017). Furthermore, the Variance Inflation Factor (VIF) of the fitted models was determined using the `vif.mer()` function of the **lme4** package to investigate possible collinearity between fixed effects. For VIF numbers below a threshold of 3, collinearity is thought to not be of concern (Zuur et al., 2009). By displaying the model residuals against the fitted values, I verified the assumptions of homogeneous and normally distributed residuals.

Effects of food availability on movement parameter on a focal level

Focals that were tracked numerous times can greatly impact the results of the described models. I selected five of the most-tracked females from two families to detect potential opposing trends in their behavior. Focals Ellie and her mother Friska represented one matriline, and Lilly, Lisa, and Cissy the other matriline. In a final step, I assessed and visually inspected correlations between the values of eFAI, fruit eFAI, non-fruit eFAI, and hFAI and the values of the movement parameters DJL and sinuosity on this focal level. Because of a limited number of follows I fitted no further models on a focal level.

4.2 Results

In Appendix C (Figure C.1), an overview of all scatterplots and Pearson's correlation coefficients are included showing movement parameters (response effects) and representations of food availability (fixed effects).

4.2.1 Overview of movement parameter for the different age-sex classes

The total number of analyzed NN follows was 648. 315 of them were of adult females, 146 of flanged males, 122 of independent immatures, and 65 of unflanged males. An overview per age-sex class for the different calculated movement parameters, the follow durations, the sampling rates, and the number of feeding trees and range points is given in Table 4.2 and per focal in Table C.1.

TABLE 4.2: Overview of movement parameters for the four age-sex classes and nest-to-nest follows.

class	# follows	* DJL [m]	* TDD [m]	* SI	* Sinuosity	* speed [km/h]	length	* trees	points	sampling rate
unflanged male	65	948±369	419±249	0.44±0.18	0.21±0.06	0.085±0.03	11:09:59	19	22.1	00:29:14
independent immature	122	901±287	394±201	0.44±0.17	0.21±0.06	0.081±0.02	11:00:42	20	21.5	00:29:26
flanged male	146	858±356	464±278	0.53±0.19	0.22±0.06	0.078±0.03	10:53:42	16	21.5	00:29:10
adult female	315	772±220	377±194	0.48±0.18	0.23±0.06	0.07±0.02	11:00:14	18	21.6	00:29:18

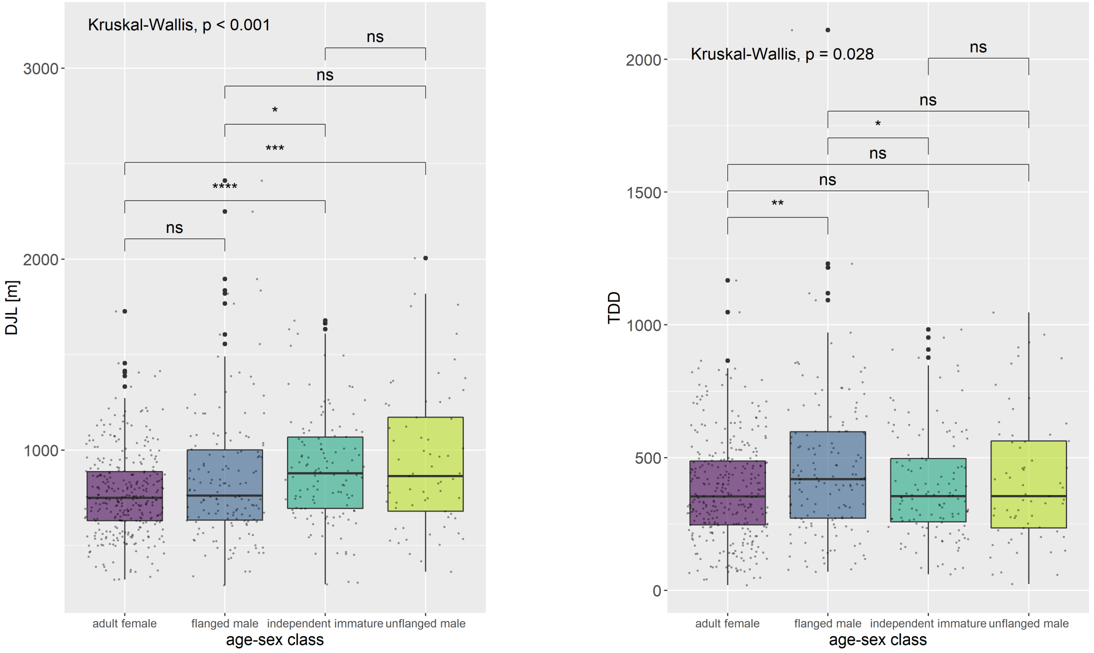
*: difference between age-sex classes are on significance level

The average sampling rate between GPS points was slightly shorter than 30 minutes because morning and night nests were included in NN follows, and the normalization of range points is always on the half hour. Therefore, the time from the first to the second GPS point and from the second last to the last can deviate from a 30-minute interval. However, there were no significant differences in the sampling rate between the age-sex classes (Kruskal Wallis, df = 3, $\chi^2 = 3.73$, p = 0.29). On average, the follows consisted of 21.6 range points and 18.3 feeding trees.

I analyzed the derived movement parameters for differences between age-sex classes (Table 4.2). On average, DJL was 833.51 ±291.58 m. There was a significant difference in DJL between age-sex classes (Kruskal Wallis, df = 3, $\chi^2 = 25.20$, $p < 0.001$). Independent immatures and unflanged males had significantly longer DJL than flanged males and adult females, which had less variation in DJL (Figure 4.1a). Unflanged males had, on average, around 175 m longer DJL than adult females.

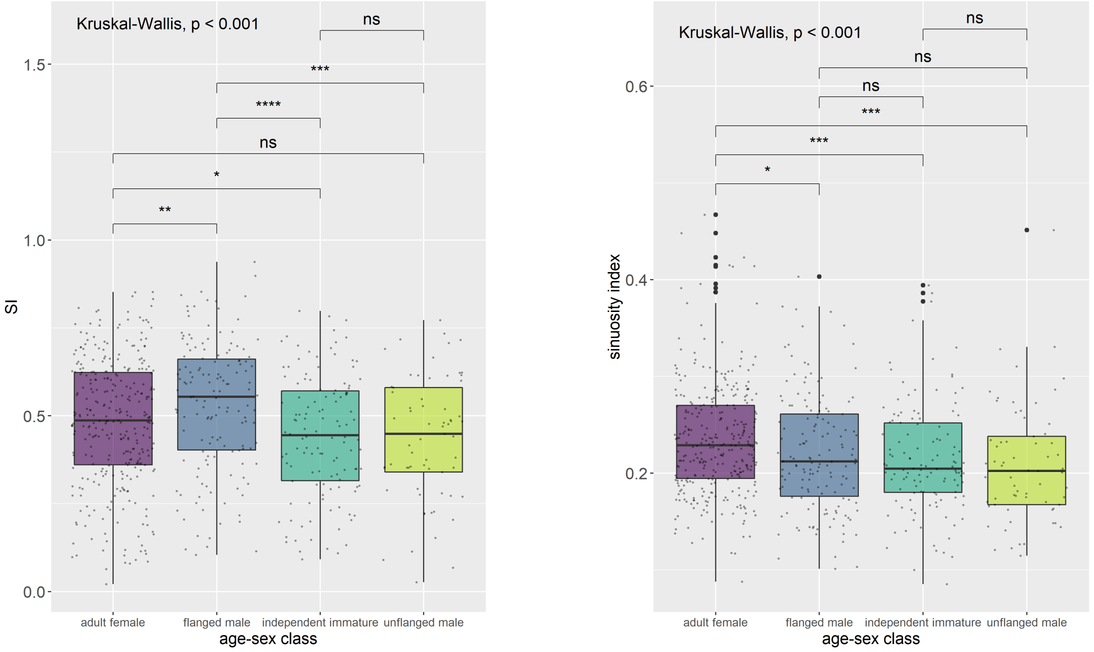
TDDs between morning and night nests were significantly different between age-sex classes (Kruskal Wallis, df = 3, $\chi^2 = 9.09$, p = 0.028). On average, TDD was 404.22 ±224.70 m. Males had longer TDDs than females, yet, not statistically significant. However, flanged males showed significantly longer TDDs than adult females and independent immatures (Figure 4.1b).

Subsequently, the SI, calculated from TDD and DJL (Section 4.1.1), differed between age-sex classes (Kruskal Wallis, df = 3, $\chi^2 = 20.46$, $p < 0.001$). Mainly, SI values from flanged males were significantly higher than from all other age-sex classes, meaning their movement paths were straighter. Furthermore, adult females also tended towards higher SI values compared to independent immatures and unflanged males. However, the difference to the latter was not statistically significant (Figure 4.2a).



(A) (B)

FIGURE 4.1: DJL (**A**) and TDD (**B**) for the four different analyzed age-sex classes. Pairwise Wilcoxon signed rank (WSR) tests and overall a Kruskal-Wallis test were performed. Significance levels: $^{****}p < 0.0001$; $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; ns $p > 0.05$.



(A) (B)

FIGURE 4.2: SI (**A**) and sinuosity (**B**) for the four different analyzed age-sex classes. Pairwise Wilcoxon signed rank (WSR) tests and overall a Kruskal-Wallis test were performed. Significance levels: $^{****}p < 0.0001$; $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; ns $p > 0.05$.

The sinuosity index as a tortuosity value was also significantly different for age-sex classes (Kruskal Wallis, df = 3, $\chi^2 = 19.70$, $p < 0.001$). Sinuosity values were highest for adult females, with a statistically significant difference to all other age-sex classes. Independent immatures and unflanged males showed the lowest but similar sinuosity values (Figure 4.2b).

Furthermore, the speed, calculated from the DJL and the length of the follow was significantly different for age-sex classes. Unflanged males moved significantly faster than independent immatures and flanged males, while adult females moved significantly slower than all other age-sex classes (Table 4.2).

4.2.2 Effects of food availability on daily movement

First, the mean sampling rate of the follows had no significant influence on DJL (Spearman's rho, $r_s = 0.007$, $p = 0.85$), sinuosity (Spearman's rho, $r_s = -0.054$, $p = 0.18$) and the other two movement parameters, TDD (Spearman's rho, $r_s = -0.072$, $p = 0.07$) and SI (Spearman's rho, $r_s = -0.051$, $p = 0.20$). Therefore, I excluded the mean sampling rate as a fixed effect in the linear mixed-effects models. Furthermore, the resulting VIF for all fixed effects in all models were not a problem as they ranged between 1 and 1.5, which expresses small collinearity.

Day journey length

When comparing the model RO_DJL to the respective null model, I found that RO_DJL fitted the data significantly better (LRT, $p < 0.001$, $\chi^2 = 23.84$). RO_DJL showed a significant trend for an effect of age-sex class on DJL (Table 4.3a), which is in line with what was already discovered in Section 4.2.1. The results indicated a large effect size in that unflanged males were estimated to travel 140 m further, and independent immatures were predicted to move 127 m more than adult females. In contrast, flanged males were predicted not to differ significantly from adult females in terms of DJL. RO_DJL provided no evidence for a significant effect of hFAI and fruit eFAI on DJL, whereas the effect of non-fruit eFAI on DJL was significant ($p < 0.01$). The effect size was strong and in a negative direction.

The proportion of the variance in DJL explained by the random effect focal was 32% and 17.5% for month-year groups, when only random effect models were used, respectively (see ICC). Therefore, differences between individual orangutans and the different months explain more variation in DJL than the fixed effects. Overall, all factors explained around 38.5% of variation in DJL (conditional $R^2 = 0.385$), whereas only the fixed effects could explain around 7.4% (marginal $R^2 = 0.074$).

Likewise, the FO_DJL model fitted the data significantly better than the respective null model (LRT, $p < 0.001$, $\chi^2 = 34.16$). Effects of age-sex classes and non-fruit eFAI were significant, whereas hFAI and fruit eFAI still provided no evidence for significant effects (Table C.2a).

RM_DJL and RF_DJL models fitted the data significantly better than their respective null models (LRT, $p < 0.01$, $\chi^2 = 12.20$ and LRT, $p = 0.046$, $\chi^2 = 7.99$). Males were predicted to travel, on average, 651 m per day, whereas females were predicted to travel, on average, 814 m per day. For males and females, neither hFAI, fruit eFAI, nor non-fruit eFAI had a significant effect on DJL. When analyzing the effect of different food availability on DJL separately, the fixed effects in the models explained less variation in DJL for males (marginal R^2 = 0.060) and females (marginal R^2 = 0.030) than in the RO_DJL model (Table 4.3b and c). For females, almost half of the variance in DJL could be explained when all effects were included in the RF_DJL model (conditional R^2 = 0.479).

TABLE 4.3: Statistical reduced models trying to explain the Day Journey Length (DJL) overall and for males and females separately. 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 stem from an ANOVA of random effect deletion.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	DJL of all age-sex classes (RO_DJL)	Intercept ***	Intercept	740.27	507.59 – 972.95	**<0.001**	-
	n = 625	hFAI	Fixed	8.85	-1.45 – 19.15	0.097	1.11
	p < 0.001 * **	fruit eFAI	Fixed	193.41	-57.61 – 444.42	0.137	1.12
	M-R^2 = 0.074	non-fruit eFAI **	Fixed	-355.98	-591.73 – -120.23	**<0.01**	1.09
	C-R^2 = 0.385	Adult female - Flanged male	Fixed	18.90	-104.67 – 142.47	0.767	1.48
	Family = Gaussian	Adult female - Independent immature *	Fixed	126.62	26.60 – 226.63	**0.014**	1.26
		Adult female - Unflanged male *	Fixed	139.76	9.78 – 269.73	**0.039**	1.48
		Focal ***	Random	-	-	**<0.001**	-
		Month Year ***	Random	-	-	**<0.001**	-
b)	DJL of all males (RM_DJL)	Intercept **	Intercept	651.08	212.44 – 1089.71	**<0.01**	-
	n = 246	hFAI	Fixed	17.42	-1.46 – 36.30	0.079	1.26
	**p < 0.01 ** **	fruit eFAI	Fixed	343.73	-144.33 – 831.79	0.176	1.11
	M-R^2 = 0.060	non-fruit eFAI	Fixed	-385.77	-794.40 – 22.87	0.073	1.22
	C-R^2 = 0.280	Focal ***	Random	-	-	**<0.001**	-
	Family = Gaussian	Month Year	Random	-	-	0.396	-
c)	DJL of all females (RF_DJL)	Intercept ***	Intercept	813.50	579.51 – 1047.50	**<0.001**	-
	n = 379	hFAI	Fixed	3.07	-7.56 – 13.70	0.574	1.08
	**p = 0.046 * **	fruit eFAI	Fixed	203.10	-45.35 – 451.55	0.116	1.11
	M-R^2 = 0.030	non-fruit eFAI	Fixed	-248.06	-494.17 – -1.95	0.053	1.05
	C-R^2 = 0.479	Focal ***	Random	-	-	**<0.001**	-
	Family = Gaussian	Month Year ***	Random	-	-	**<0.001**	-

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

The full models FM_DJL and FF_DJL fitted the data significantly better than their respective null models (LRT, $p < 0.01$, χ^2 = 14.19 and LRT, $p < 0.01$, χ^2 = 12.23). For males, non-fruit eFAI had a significant negative effect on DJL with large effect size, whereas neither fruit eFAI nor hFAI showed an effect on DJL (Table C.2b and c). Furthermore, for females, fruit eFAI had a significant positive effect on DJL, whereas neither hFAI nor non-fruit eFAI affected DJL.

Looking at the age-sex class models, RFM_DJL, RUM_DJL, and RII_DJL did not perform better than their respective null models. Only the RAF_DJL model fitted the data significantly better than the respective null model (LRT, $p < 0.01$, χ^2 = 13.45). Non-fruit eFAI was found to have a significant negative effect on DJL, whereas neither hFAI nor fruit eFAI did have a significant effect on DJL (Table 4.4b). For adult females, an increase in non-fruit eFAI was estimated to have a strong negative effect on DJL. Fixed effects could explain 6.5% of the variation in DJL. The conditional R^2 value was 53.2%, and both random effects were found to be significant contributors to the model.

The full models FFM_DJL (LRT, p = 0.039, χ^2 = 8.35), FAF_DJL (LRT, $p < 0.001$, χ^2 = 16.63), and FUM_DJL (LRT, p = 0.050, χ^2 = 7.81) performed better than their respective null models, whereas FII_DJL did not. In the FFM_DJL and FUM_DJL models only non-fruit eFAI had a significant negative effect on DJL (Table C.3a and c). In the FAF_DJL model fruit eFAI had a significant positive effect and non-fruit eFAI a significant negative effect (Table C.3b). hFAI had no effect in any of the full models. Compared to the reduced models, similar values in DJL were predicted for adult females and unflanged males, whereas much higher DJLs were predicted for flanged males (822 m) and independent immatures (1081 m).

TABLE 4.4: Statistical reduced models trying to explain the Day Journey Length (DJL) for all four age-sex classes separately.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	DJL of flanged males only (RFM_DJL)	Intercept	Intercept	546.04	-5.23 – 1097.32	0.061	-
	n = 143	hFAI	Fixed	19.90	-3.36 – 43.15	0.103	1.33
	p = 0.065	fruit eFAI	Fixed	309.14	-329.34 – 947.62	0.350	1.12
	M-R^2 = 0.049	non-fruit eFAI	Fixed	-289.81	-793.74 – 214.11	0.270	1.22
	C-R^2 = 0.240	Focal *	Random	-	-	**0.017**	-
	Family = Gaussian	Month Year	Random	-	-	0.946	-
b)	DJL of adult females only (RAF_DJL)	Intercept ***	Intercept	811.30	555.82 – 1066.78	**<0.001**	-
	n = 313	hFAI	Fixed	6.90	-4.39 – 18.20	0.238	1.05
	p < 0.01 **	fruit eFAI	Fixed	147.30	-125.20 – 419.81	0.296	1.14
	M-R^2 = 0.065	non-fruit eFAI **	Fixed	-415.93	-686.66 – -145.20	**<0.01**	1.09
	C-R^2 = 0.532	Focal **	Random	-	-	**<0.01**	-
	Family = Gaussian	Month Year ***	Random	-	-	**<0.001**	-
c)	DJL of unflanged males only (RUM_DJL)	Intercept *	Intercept	1127.17	126.63 – 2127.71	**0.039**	-
	n = 57	hFAI	Fixed	0.69	-45.11 – 46.48	0.977	1.20
	p = 0.165	fruit eFAI	Fixed	323.28	-812.72 – 1459.28	0.584	1.09
	M-R^2 = 0.099	non-fruit eFAI	Fixed	-887.76	-1911.84 – 136.33	0.105	1.30
	C-R^2 = 0.487	Focal	Random	-	-	0.302	-
	Family = Gaussian	Month Year	Random	-	-	0.188	-
d)	DJL of independent immatures only (RII_DJL)	Intercept **	Intercept	840.26	360.24 – 1320.27	**<0.01**	-
	n = 112	hFAI	Fixed	5.77	-16.50 – 28.04	0.615	1.14
	p = 0.921	fruit eFAI	Fixed	98.58	-442.44 – 639.60	0.724	1.08
	M-R^2 = 0.005	non-fruit eFAI	Fixed	-66.10	-571.08 – 438.89	0.799	1.05
	C-R^2 = 0.275	Focal *	Random	-	-	**0.011**	-
	Family = Gaussian	Month Year	Random	-	-	0.338	-

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

Total displacement distance

None of the reduced models RO_TDD, RM_TDD, and RF_TDD fitted the data significantly better than their respective null models (Table 4.5a-c). Also, the full models FO_TDD and FF_TDD did not perform better than their respective null models. Only the model for males FM_TDD fitted the data significantly better than the respective null model (LRT, p = 0.013, χ^2 = 10.77). Non-fruit eFAI had a significant effect on TDD with a large negative effect size (Table C.4b). Fruit eFAI and hFAI showed no effect on TDD. The fixed effects could explain 4.7% of the variation in TDD. In contrast, the conditional R^2 value was 24.4%, and only the random effect focal was found to contribute to the model significantly.

Also, none of the reduced models for the age-sex classes (RFM_TDD, RAF_TDD, RUM_TDD, and RII_TDD) fitted the data significantly better than their respective null models (Table 4.6a-d). The same can be said about the full models for the age-sex classes (FFM_TDD, FAF_TDD, FUM_TDD, and FII_TDD), even though the FFM_TDD model was close to a significance level (Table C.5a).

TABLE 4.5: Statistical reduced models trying to explain Total Displacement Distance (TDD) overall and for males and females separately.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	TDD of all age-sex classes (RO_TDD)	Intercept ***	Intercept	391.16	207.55 – 574.78	**<0.001**	-
	n = 625	hFAI	Fixed	2.82	-5.37 – 11.02	0.503	1.11
	p = 0.371	fruit eFAI	Fixed	9.01	-191.10 – 209.11	0.930	1.11
	M-R^2 = 0.028	non-fruit eFAI	Fixed	-130.45	-317.97 – 57.07	0.178	1.09
	C-R^2 = 0.288	Adult female - Flanged male	Fixed	77.33	-13.53 – 168.20	0.104	1.44
	Family = Gaussian	Adult female - Independent immature	Fixed	10.35	-66.80 – 87.50	0.793	1.27
		Adult female - Unflanged male	Fixed	40.15	-57.55 – 137.86	0.424	1.42
		Focal ***	Random	-	-	**<0.001**	-
		Month Year **	Random	-	-	**<0.01**	-
b)	TDD of all males (RM_TDD)	Intercept *	Intercept	365.63	63.85 – 667.41	**0.018**	-
	n = 246	hFAI	Fixed	8.93	-4.08 – 21.94	0.180	1.25
	p = 0.141	fruit eFAI	Fixed	77.32	-258.84 – 413.48	0.653	1.11
	M-R^2 = 0.031	non-fruit eFAI	Fixed	-230.42	-509.36 – 48.53	0.107	1.22
	C-R^2 = 0.204	Focal **	Random	-	-	**<0.01**	-
	Family = Gaussian	Month Year	Random	-	-	1	-
c)	TDD of all females (RF_TDD)	Intercept ***	Intercept	393.14	197.44 – 588.84	**<0.001**	-
	n = 379	hFAI	Fixed	0.43	-8.73 – 9.60	0.927	1.09
	p = 0.983	fruit eFAI	Fixed	7.36	-208.45 – 223.18	0.947	1.10
	M-R^2 = 0.0007	non-fruit eFAI	Fixed	-37.08	-249.17 – 175.01	0.734	1.05
	C-R^2 = 0.226	Focal *	Random	-	-	**0.011**	-
	Family = Gaussian	Month Year **	Random	-	-	**<0.01**	-

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

TABLE 4.6: Statistical reduced models trying to explain Total Displacement Distance (TDD) for all four age-sex classes separately.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	TDD of flanged males only (RFM_TDD)	Intercept *	Intercept	490.66	58.27 – 923.06	**0.028**	-
	n = 143	hFAI	Fixed	6.52	-11.71 – 24.76	0.484	1.33
	p = 0.334	fruit eFAI	Fixed	-79.54	-580.00 – 420.92	0.756	1.11
	M-R^2 = 0.022	non-fruit eFAI	Fixed	-227.14	-621.97 – 167.70	0.261	1.22
	C-R^2 = 0.226	Focal **	Random	-	-	**<0.01**	-
	Family = Gaussian	Month Year	Random	-	-	1	-
b)	TDD of adult females only (RAF_TDD)	Intercept **	Intercept	371.35	146.51 – 596.19	**<0.01**	-
	n = 313	hFAI	Fixed	3.44	-7.05 – 13.93	0.525	1.05
	p = 0.798	fruit eFAI	Fixed	20.04	-239.19 – 279.27	0.880	1.13
	M-R^2 = 0.006	non-fruit eFAI	Fixed	-78.15	-320.54 – 164.23	0.532	1.08
	C-R^2 = 0.188	Focal	Random	-	-	1	-
	Family = Gaussian	Month Year **	Random	-	-	**<0.01**	-
c)	TDD of unflanged males only (RUM_TDD)	Intercept	Intercept	336.15	-294.20 – 966.51	0.310	-
	n = 57	hFAI	Fixed	10.07	-19.62 – 39.77	0.513	1.18
	p = 0.309	fruit eFAI	Fixed	224.10	-488.15 – 936.35	0.548	1.08
	M-R^2 = 0.065	non-fruit eFAI	Fixed	-324.47	-971.80 – 322.86	0.340	1.26
	C-R^2 = 0.279	Focal	Random	-	-	1	-
	Family = Gaussian	Month Year	Random	-	-	0.322	-
d)	TDD of independent immatures only (RII_TDD)	Intercept	Intercept	224.62	-131.77 – 581.01	0.226	-
	n = 112	hFAI	Fixed	2.75	-13.77 – 19.28	0.746	1.17
	p = 0.754	fruit eFAI	Fixed	176.78	-226.67 – 580.22	0.398	1.09
	M-R^2 = 0.015	non-fruit eFAI	Fixed	131.18	-244.27 – 506.63	0.499	1.07
	C-R^2 = 0.311	Focal *	Random	-	-	**0.034**	-
	Family = Gaussian	Month Year	Random	-	-	0.192	-

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

4.2.3 Effects of food availability on the tortuosity in movement paths

Sinuosity index

Besides looking at the possible influence of fruit and food availability on DJL and TDD, the focus was also on finding possible effects on the tortuosity indices sinuosity and straightness. When comparing the model RO_sinuosity to the respective null model, I found that RO_sinuosity fitted the data significantly better (LRT, p = 0.032, χ^2 = 13.80). Sinuosity was estimated to be 0.26. No clear differences between adult females and all other age-sex classes were found in the model compared to what was noticed in Section 4.2.1. Fruit eFAI had a significant effect on the sinuosity (p < 0.05) (Table 4.7a). The effect was strongly negative. Non-fruit eFAI and hFAI showed no significant effect. The proportion of the variance in sinuosity explained by focals was 12.3% and 15.1% for month-year groups when only random effect models were used, respectively (see ICC). Fixed effects could only explain around 4.3% of variation in the sinuosity (marginal R^2 = 0.043), whereas all factors explained 22.7% (conditional R^2 = 0.227).

Also, the FO_sinuosity model fitted the data significantly better than the respective null model (LRT, p < 0.01, χ^2 = 19.25). Effects of age-sex classes and fruit eFAI were significant, whereas hFAI and non-fruit eFAI showed no significant effects (Table C.6a).

Neither the RM_sinuosity nor the RF_sinuosity model fitted the data significantly better than their respective null models (Table 4.7b and c). However, the full model FF_sinuosity fitted the data significantly better than the respective null models (LRT, p = 0.013, χ^2 = 10.70), whereas the full model FM_sinuosity did not. For females, the sinuosity was predicted to be 0.258. Fruit eFAI significantly affected the sinuosity of females with a large negative effect size. In contrast, neither fruit eFAI nor hFAI showed an effect on the sinuosity of females (Table C.6c).

TABLE 4.7: Statistical reduced models trying to explain sinuosity of all age-sex classes and for males and females separately.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	Sinuosity of all age-sex classes (RO_sinuosity)	Intercept ***	Intercept	0.2600	0.2100 – 0.3100	**<0.001**	-
	n = 625	hFAI	Fixed	-0.0014	-0.0037 – 0.0009	0.233	1.12
	p = 0.032 *	fruit eFAI *	Fixed	-0.0590	-0.1148 – -0.0032	**0.042**	1.11
	M-R^2 = 0.043	non-fruit eFAI	Fixed	0.0388	-0.0129 – 0.0904	0.146	1.09
	C-R^2 = 0.227	Adult female - Flanged male	Fixed	-0.0040	-0.0228 – 0.0149	0.683	1.36
	Family = Gaussian	Adult female - Independent immature	Fixed	-0.0128	-0.0303 – 0.0047	0.158	1.27
		Adult female - Unflanged male	Fixed	-0.0204	-0.0420 – 0.0011	0.068	1.32
		Focal **	Random	-	-	**<0.01**	-
		Month Year ***	Random	-	-	**<0.001**	-
b)	Sinuosity of all males (RM_sinuosity)	Intercept ***	Intercept	0.2446	0.1669 – 0.3222	**<0.001**	-
	n = 246	hFAI	Fixed	-0.0021	-0.0055 – 0.0013	0.227	1.26
	p = 0.141	fruit eFAI	Fixed	-0.0326	-0.1197 – 0.0544	0.467	1.11
	M-R^2 = 0.029	non-fruit eFAI	Fixed	0.0471	-0.0253 – 0.1196	0.211	1.22
	C-R^2 = 0.169	Focal *	Random	-	-	**0.017**	-
	Family = Gaussian	Month Year	Random	-	-	0.405	-
c)	Sinuosity of all females (RF_sinuosity)	Intercept ***	Intercept	0.2582	0.2001 – 0.3163	**<0.001**	-
	n = 379	hFAI	Fixed	-0.0008	-0.0035 – 0.0019	0.572	1.09
	p = 0.053	fruit eFAI *	Fixed	-0.0777	-0.1419 – -0.0134	**0.022**	1.10
	M-R^2 = 0.040	non-fruit eFAI	Fixed	0.0327	-0.0301 – 0.0956	0.312	1.05
	C-R^2 = 0.270	Focal *	Random	-	-	**0.038**	-
	Family = Gaussian	Month Year ***	Random	-	-	**<0.001**	-

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

TABLE 4.8: Statistical reduced models trying to explain sinuosity for all four age-sex classes separately.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	Sinuosity of flanged males only (RFM_sinuosity)	Intercept ***	Intercept	0.2501	0.1575 – 0.3426	**<0.001**	-
	n = 143	hFAI	Fixed	-0.0023	-0.0062 – 0.0016	0.251	1.33
	p = 0.155	fruit eFAI	Fixed	-0.0367	-0.1440 – 0.0706	0.504	1.11
	M-R^2 = 0.038	non-fruit eFAI	Fixed	0.0579	-0.0267 – 0.1424	0.182	1.22
	C-R^2 = 0.227	Focal **	Random	-	-	**<0.01**	-
	Family = Gaussian	Month Year	Random	-	-	0.999	-
b)	Sinuosity of adult females only (RAF_sinuosity)	Intercept ***	Intercept	0.2909	0.2272 – 0.3546	**<0.001**	-
	n = 313	hFAI	Fixed	-0.0019	-0.0048 – 0.0011	0.228	1.05
	p = 0.025 *	fruit eFAI *	Fixed	-0.0978	-0.1713 – -0.0243	**0.013**	1.13
	M-R^2 = 0.059	non-fruit eFAI	Fixed	0.0234	-0.0453 – 0.0922	0.508	1.08
	C-R^2 = 0.213	Focal	Random	-	-	1	-
	Family = Gaussian	Month Year ***	Random	-	-	**<0.001**	-
c)	Sinuosity of unflanged males only (RUM_sinuosity)	Intercept *	Intercept	0.1818	0.0428 – 0.3209	**0.014**	-
	n = 57	hFAI	Fixed	0.0010	-0.0057 – 0.0077	0.776	1.19
	p = 0.480	fruit eFAI	Fixed	-0.0338	-0.1856 – 0.1179	0.664	1.07
	M-R^2 = 0.043	non-fruit eFAI	Fixed	0.0966	-0.0449 – 0.2381	0.188	1.26
	C-R^2 = 0.073	Focal	Random	-	-	0.766	-
	Family = Gaussian	Month Year	Random	-	-	1	-
d)	Sinuosity of independent immatures only (RII_sinuosity)	Intercept ***	Intercept	0.2115	0.1109 – 0.3121	**<0.001**	-
	n = 112	hFAI	Fixed	0.0003	-0.0043 – 0.0050	0.892	1.17
	p = 0.997	fruit eFAI	Fixed	-0.0027	-0.1158 – 0.1104	0.963	1.09
	M-R^2 = 0.0004	non-fruit eFAI	Fixed	0.0061	-0.0980 – 0.1102	0.909	1.07
	C-R^2 = 0.223	Focal	Random	-	-	0.221	-
	Family = Gaussian	Month Year	Random	-	-	0.068	-

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

Regarding the reduced age-sex class models, RFM_sinuosity, RUM_sinuosity, and RII_sinuosity did not perform better than their respective null models. Only the RAF_sinuosity model fitted the data significantly better than the respective null model (LRT, p = 0.025, χ^2 = 9.35). Adult females were predicted to have high sinuosity values (0.291) (Table 4.8b). Fruit eFAI was found to have a significant negative effect on the sinuosity of adult females, whereas neither hFAI nor non-fruit eFAI had a significant effect. Fixed effects could explain 5.9% of the variation in the sinuosity of adult females. The conditional R^2 value was 21.3%, and only the random effect month-year was found to be a significant contributor to the model.

Likewise, the full models FFM_sinuosity, FUM_sinuosity, and FII_sinuosity did not perform better than their respective null models. Again, only the FAF_sinuosity model performed significantly better than the respective null model (LRT, p <0.01, χ^2 = 12.48). Adult females were predicted to have a higher sinuosity value (0.31) than in the RAF_sinuosity model. Fruit eFAI had a significant effect on the sinuosity of adult females with a large negative effect size (Table C.7b). Non-fruit eFAI and hFAI had no significant effect in the FAF_sinuosity model. Fixed effects could explain 6.8% of the variation in the sinuosity of adult females.

Straightness index

When comparing the model RO_SI to the respective null model, I found that RO_SI fitted the data significantly better (LRT: p = 0.013, χ^2 = 16.11). Flanged males were estimated on a significant level to move straighter than adult females (Table 4.9a). However, food availability did not affect the straightness of movement significantly. Also, the full model FO_SI performed better than the respective null model (LRT: p = 0.016, χ^2 = 15.62). None of the fixed effects showed a significance (Table C.8a). Neither the reduced models RM_SI and RF_SI (Table 4.9b and c) nor the full models FM_SI and FF_SI (Table C.8b and c) fitted the data significantly better than their respective null model.

TABLE 4.9: Statistical reduced models trying to explain the Straightness Index (SI) overall and for males and females separately.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	SI of all age-sex classes (RO_SI)	Intercept ***	Intercept	0.5017	0.3749 – 0.6285	**<0.001**	-
	n = 625	hFAI	Fixed	-0.0018	-0.0075 – 0.0039	0.547	1.11
	p = 0.013 *	fruit eFAI	Fixed	-0.0643	-0.2040 – 0.0755	0.372	1.12
	M-R^2 = 0.043	non-fruit eFAI	Fixed	0.0576	-0.0729 – 0.1880	0.391	1.10
	C-R^2 = 0.167	Adult female - Flanged male *	Fixed	0.0642	0.0035 – 0.1249	**0.047**	1.37
	Family = Gaussian	Adult female - Independent immature	Fixed	-0.0469	-0.1027 – 0.0088	0.103	1.28
		Adult female - Unflanged male	Fixed	-0.0361	-0.1048 – 0.0326	0.308	1.32
		Focal **	Random	-	-	**<0.01**	-
		Month Year	Random	-	-	0.208	-
b)	SI of all males (RM_SI)	Intercept ***	Intercept	0.5476	0.3229 – 0.7723	**<0.001**	-
	n = 246	hFAI	Fixed	-0.0008	-0.0105 – 0.0088	0.865	1.26
	p = 0.141	fruit eFAI	Fixed	-0.0518	-0.3012 – 0.1976	0.686	1.11
	M-R^2 = 0.005	non-fruit eFAI	Fixed	-0.0518	-0.3142 – 0.1016	0.324	1.22
	C-R^2 = 0.237	Focal ***	Random	-	-	**<0.001**	-
	Family = Gaussian	Month Year	Random	-	-	0.824	-
c)	SI of all females (RF_SI)	Intercept ***	Intercept	0.4932	0.3516 – 0.6348	**<0.001**	-
	n = 379	hFAI	Fixed	-0.0020	-0.0087 – 0.0047	0.562	1.07
	p = 0.219	fruit eFAI	Fixed	-0.0954	-0.2529 – 0.0620	0.244	1.10
	M-R^2 = 0.014	non-fruit eFAI	Fixed	0.1044	-0.0508 – 0.2596	0.196	1.05
	C-R^2 = 0.073	Focal	Random	-	-	0.285	-
	Family = Gaussian	Month Year	Random	-	-	0.480	-

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

Lastly, none of the reduced models for the age-sex classes (RFM_SI, RAF_SI, RUM_SI, and RII_SI) fitted the data significantly better than their respective null models (Table 4.10a-d). The same can be said about the full models for the age-sex classes (FFM_SI, FAF_SI, FUM_SI, and FII_SI) (Table C.9a-d).

TABLE 4.10: Statistical reduced models trying to explain the Straightness Index (SI) for all four age-sex classes separately.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	SI of flanged males only (RFM_SI)	Intercept **	Intercept	0.5909	0.2398 – 0.9421	**<0.01**	-
	n = 143	hFAI	Fixed	-0.0000	-0.0150 – 0.0149	0.995	1.32
	p = 0.938	fruit eFAI	Fixed	-0.1222	-0.5277 – 0.2834	0.558	1.14
	M-R^2 = 0.004	non-fruit eFAI	Fixed	0.0148	-0.3063 – 0.3359	0.929	1.18
	C-R^2 = 0.246	Focal *	Random	-	-	**0.040**	-
	Family = Gaussian	Month Year *	Random	-	-	**0.032**	-
b)	SI of adult females only (RAF_SI)	Intercept ***	Intercept	0.4843	0.3221 – 0.6464	**<0.001**	-
	n = 313	hFAI	Fixed	-0.0029	-0.0106 – 0.0047	0.460	1.04
	p = 0.277	fruit eFAI	Fixed	-0.0504	-0.2372 – 0.1364	0.601	1.15
	M-R^2 = 0.017	non-fruit eFAI	Fixed	0.1402	-0.0399 – 0.3204	0.137	1.11
	C-R^2 = 0.074	Focal	Random	-	-	0.678	-
	Family = Gaussian	Month Year	Random	-	-	0.383	-
c)	SI of unflanged males only (RUM_SI)	Intercept	Intercept	0.3685	-0.1076 – 0.8446	0.142	-
	n = 57	hFAI	Fixed	0.0026	-0.0195 – 0.0248	0.816	1.18
	p = 0.988	fruit eFAI	Fixed	0.0582	-0.4896 – 0.6060	0.837	1.08
	M-R^2 = 0.002	non-fruit eFAI	Fixed	0.0280	-0.4622 – 0.5182	0.912	1.27
	C-R^2 = 0.421	Focal	Random	-	-	1	-
	Family = Gaussian	Month Year	Random	-	-	0.085	-
d)	SI of independent immatures only (RII_SI)	Intercept	Intercept	0.3136	0.0109 – 0.6163	0.053	-
	n = 112	hFAI	Fixed	0.0010	-0.0130 – 0.0151	0.885	1.17
	p = 0.854	fruit eFAI	Fixed	0.1200	-0.2223 – 0.4624	0.500	1.09
	M-R^2 = 0.013	non-fruit eFAI	Fixed	0.1170	-0.2021 – 0.4360	0.479	1.07
	C-R^2 = 0.309	Focal *	Random	-	-	**0.033**	-
	Family = Gaussian	Month Year	Random	-	-	0.323	-

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

4.2.4 Effects of food availability on movement parameter on a focal level

Results indicated that different trends could be observed on a focal level for DJL (Figure C.4). I detected significant correlations for fruit eFAI and non-fruit eFAI with DJL in opposite directions, for example, for the focals Lisa and her mother Cissy. In contrast, for the younger mothers Ellie and Lilly, I discovered positive trends for both indices (Figures C.4c and C.4d). When looking at the sinuosity of the five selected adult females, again significant correlations for fruit eFAI and non-fruit eFAI in opposite directions could be observed for the focals Lisa and her mother Cissy, whereas for the younger mothers, Ellie and Lilly, the trends were negative for both indices (Figures C.7c and C.7d).

4.3 Discussion

4.3.1 How do the age-sex classes differ in their movement?

The first research question for this Chapter 4 assessed the differences between the age-sex classes regarding their movement parameters (**RQ B.1**). I predicted differences for the four age-sex classes regarding their daily movement and tortuosity based on the information from the literature (Graf, 2021; Schuppli et al., 2016a; Singleton et al., 2009). As a matter of fact, all of the movement parameters significantly differed between the age-sex classes (Table 4.2 and Figures 4.1 and 4.2).

Generally, my findings for DJL are in line with my predictions and the results from Graf (2021) and Singleton et al. (2009). I found the lowest average DJL for adult females (772 ±220 m) (Section 4.2.1), which were shorter than the ones in Graf (2021) with 858 ±323 m and Singleton et al. (2009) with 830 ±306 m. However, this result differs from the result in the study site Tuanan on Borneo, where flanged males had the lowest DJL of around 670 m (Vogel et al., 2017), which was suggested to be linked to an energy conservation strategy when facing fruit scarcity. For Suaq, such a strategy may not be required as orangutans almost always have some trees around that bear fruit. This likely results in a near-constant positive energy balance and allows flanged males to move further according to a 'search and find' strategy (Morrogh-Bernard et al., 2009). Based on the description of Morrogh-Bernard et al. (2009), such a strategy is used when orangutans rest little and mainly feed or move in search of food to maximize their energy intake because they are not energetically restricted in their movement.

Similar to Graf (2021), I found, on average, the longest DJL for unflanged males, followed by the independent immatures and flanged males. Those differences between the age-sex classes originate from different reproductive and mating strategies (Utami Atmoko et al., 2009). However, differences in the distance values to the study of Graf (2021) might be explained by more included follows, updated data or differing data cleaning, where follows were omitted based on the bootstrapping method, leading to a minimum number of 10 follows per month in my analysis (Section 3.1.2). The same could be valid for the differences in average TDD, where I found the longest morning-to-night nest distance for flanged males, while Graf (2021) found it for unflanged males. In contrast, in both theses, the shortest average TDD were found for adult females, which makes sense as they stay locally in their home ranges, and (flanged and unflanged) males have a broader moving range (Singleton and Schaik, 2001).

Also, I discovered similar values for the SI and sinuosity index to those in Graf (2021). Contrary to my prediction, the average sinuosity index was highest for adult females and lowest for unflanged males and independent immatures. I expected the values to be higher for the latter two age-sex classes because I assumed that they move more in a tortuous fashion and less efficiently, with less experience in the environment based on the idea of Schuppli et al. (2016a) for the age classes and the inverse straightness index. Nevertheless, one explanation for these results might be that adult females form long-term social units with their dependent offspring (Galdikas, 1985; Van Schaik, 1999). Adult females assist the dependent immatures in moving between the trees, teach them foraging skills, show them the environment, and regularly engage in social play with them (Mikeliban et al., 2021; Van Noordwijk et al., 2009). These behaviors may lead to more tortuous movement. Furthermore, higher sinuosity values for adult females would align with the results that they moved significantly slower than all other age-sex classes (Table 4.2: speed). Dependent offsprings must be carried or supported in their movement when they are young, slowing the mothers down (Van Noordwijk et al., 2009).

Regarding the SI values, I found a significant difference between adult females and independent immatures (Figure 4.2a) contradicting the results from Schuppli et al. (2016a), where they found no difference for the ramble ratio (inverse SI), which was an indicator for food locating competence. Thus, in this sense, higher SI values for adult females may indicate a higher competence to locate food sources in the forest. However, Graf (2021) has already argued that a clear interpretation of the SI values is difficult as a sampling interval of 30 minutes in the data misses a substantial portion of local tortuous movement.

4.3.2 How does food availability affect the movement of orangutans?

After establishing and analyzing a new index for a suitable representation of the experienced food availability, the main goal of this thesis was to determine how food availability, represented by hFAI, eFAI, or the two separate versions fruit eFAI and non-fruit eFAI, would affect movement parameters, such as DJL and the sinuosity of orangutans in Suaq (**RQ B.2**).

Throughout the movement analysis, I discovered opposing trends for fruit eFAI and non-fruit eFAI with DJL (Figure C.3), which canceled each other out when focusing on the whole eFAI (Figure C.2a). These trends indicate that the fruit and non-fruit availability have different, contradicting effects on the DJLs of orangutans and need to be looked at separately. Furthermore, in Chapter 3, I already compared fruit eFAI to non-fruit eFAI, and I found a negative, but not significant, trend (Figure 3.8). I further discussed that this negative trend could indicate that orangutans compensate by eating more non-fruit items when experiencing less fruit. Because of the differences I decided to include fruit eFAI and non-fruit eFAI instead of the whole eFAI in the final analysis (Section 4.1.3).

Generally, the full models for overall, sexes, and age-sex classes performed better than the reduced models in Appendix C that restricted that data set to a minimum number of 10 follows per month. The nest-to-nest follows from the additional 60 months (Section 3.2.2) increased the sample size. However, because certain months only contain a small number of follows, those monthly calculated indices values should probably be interpreted with caution, as already discussed in Section 3.3.3.

For various linear mixed-effects models, I found strong effects of the investigated factors on significant levels (Section 4.2.2). However, hFAI had no significant effect on any movement parameter in any of the models (**RQ B.2**), as predicted, probably due to generally higher fruit availability in the habitat throughout the whole year, despite showing a weak correlation with the DJL of males (Figure C.2f). This is in line with previous findings of Graf (2021) and different from studies in Tuanan and other Bornean sites, where hFAI was found to be a strong influencing and constraining factor (Ashbury, 2020; Roth et al., 2020; Wartmann, 2008). A high fruit availability in the habitat may further suggest that orangutans in Suaq have the capacity and energy to invest more in reproduction besides foraging, which has led to a high density of orangutans in Suaq (Husson et al., 2009).

Overall and sex class models

Nevertheless, the introduction of new ways to represent food availability in this thesis proved to be meaningful. Fruit and non-fruit eFAI could explain at least some variation in the DJL and sinuosity of orangutans (**RQ B.2**). For the RO_DJL and FO_DJL models, I found a significant effect of the non-fruit eFAI on DJL in a negative direction, respectively. In the models for males and females (RM_DJL and RF_DJL), food availability did not affect DJL. However, in the full model for males (FM_DJL), non-fruit eFAI, and for females (FF_DJL), fruit eFAI had a significant effect on DJL. Overall, this suggests that an increased non-fruit diet may lead to shorter DJL, but fruit eFAI seems to have a positive effect on the DJL of females only. At the same time, in the RO_sinuosity, FO_sinuosity, and FF_sinuosity models, the fruit eFAI had a significant negative effect on the sinuosity. Females seem to move in a straighter fashion when consuming more fruit items. This behavior is discussed further below (Section 4.3.3). For males, on the other hand, the variation in fruit consumption does not seem to affect their tortuosity of movement.

Furthermore, I found only in the full model for males (FM_TDD) a significant negative effect of non-fruit eFAI on the TDD of males. Hence, food availability does not affect how far female orangutans travel from nest to nest. In contrast, males have shorter TDD when they consume more non-fruit items. Also, I found no significant effects of food availability on the straightness of orangutans in any of the full or reduced models for SI. If the straightness index is used as an indicator for feeding competence (as in Schuppli et al. (2016a)), this result suggests that locating food in Suaq is not influenced by any food availability.

Age-sex class models

When looking at the age-sex class models separately, I distinguished even more pronounced trends for the DJL and the sinuosity. That confirmed the approach of splitting the models for these classes. For flanged males, non-fruit eFAI had a significant effect but only in the full models for DJL and sinuosity (FFM_DJL and FFM_sinuosity). Non-fruit eFAI had a negative effect on DJL but a positive effect on the sinuosity of flanged males, though the FFM_sinuosity model performed not better than the respective null model. Fruit eFAI had no significant effect. Morrogh-Bernard et al. (2009) suggested that flanged males may travel less because of their large body size and higher energy costs than orangutans from the other age-sex classes. Thus, when flanged males can increase their energy intake from non-fruit items, they may not need or want to travel longer distances and consequently move tortuously in a local area. This behavior may result from feeding an increased amount of time at the same location rather than switching quickly between resources (Section 3.3.4). Moreover, this behavior may be related to the mating strategy of flanged males where they do not need to travel the same distances as unflanged males in search of females (Dunkel et al., 2013; Utami Atmoko et al., 2009).

Non-fruit eFAI had a significant negative effect on the DJL of adult females (RAF_DJL and FAF_DJL) but not on their sinuosity. In contrast, fruit eFAI had a significant negative effect on the sinuosity of adult females (RAF_sinuosity and FAF_sinuosity) and a significant positive effect on their DJL (FAF_DJL). These results suggest that adult females travel longer distances when consuming more fruit but shorter distances when focusing on non-fruit items. Additionally, an increase in fruit consumption leads to a straighter movement, while an increase in non-fruit consumption does not affect their sinuosity. This behavior suggests that adult females know the locations of the fruit trees and how to move efficiently between them. Thus, adult females may move more goal-oriented and farther to find higher caloric intake fruit (Knott, 2005). However, because their diet is broader compared to all other age-sex classes (Section 3.3.2), they also consume many non-fruit items and generally don't travel that far (Section 4.3.1). Moreover, as mothers, they carry their young offspring or move after independently moving but still dependent offspring (Van Noordwijk et al., 2009). This behavior may lead to higher sinuosity and influences their movement range. However, as further discussed below, those behavioral trends can vary from individual to individual (Section 4.3.3).

In the unflanged male models, I only found a significant effect of non-fruit eFAI on DJL (FFM_DJL) but not on sinuosity. The negative effect was even larger than in the models for flanged males and adult females and suggests that unflanged males move shorter distances when increasing the amount of consumed non-fruit items. However, this trend needs to be interpreted cautiously as the significance level is around 0.05. Nevertheless, it makes sense that I discovered no effects of fruit or non-fruit food availability on daily movement and the tortuosity of unflanged males because their behavior is probably more affected by their mating strategy (Utami Atmoko et al., 2009) and not restricted by the availability of fruit. Hence, they roam in greater ranges and move faster than flanged males, as discussed in Section 4.3.1 and in Wich et al. (2009).

For independent immatures, food availability did not significantly affect DJL, TDD, sinuosity, or straightness in any models. These results suggest that daily movements of independent immatures are not defined by either fruit or non-fruit diet. It may be that for this age-sex class, social factors play a more prominent role in what way and how far they move in the habitat. For example, Galdikas (1985) showed for the research site Tanjung Puting on Borneo that independent immatures were more gregarious and social than adults. Van Noordwijk et al. (2009) found that in Suaq, they are around 30% of the time within 50 m of their mothers and an additional 30% together with other orangutans. Social tolerance was found to be higher in Suaq than at other sites (Singleton and Van Schaik, 2002). Nevertheless, another reason why no significance in the food availability is visible might be that male and female independent immatures were grouped together in one age-sex class.

Conclusively, the above-mentioned and discussed results confirm that for Suaq, the newly introduced experienced fruit availability and experienced non-fruit food availability had a more significant effect on the movement parameters DJL and sinuosity than the hFAI. However, this depended on the used model and, thus, which age-sex class I looked at. Furthermore, smaller sample sizes for independent immatures and unflanged males than for adult females and flanged males could have influenced the results.

4.3.3 Can trends be distinguished on a focal level?

After finding differences in the effects of food availability on movement parameters on the age-sex class level, I wondered about trends on the focal level. Therefore, I selected five females of different ages to look into potential differences. The oldest and most experienced females, Friska and Cissy, together with the middle-aged Lisa, had a higher mean sinuosity index than the younger mothers Ellie and especially Lilly (Table C.1). At the same time, Ellie and Lilly traveled on average longer distances during the day (DJL) than the older females, similar to what Graf (2021) had already detected. This result would mean that the trends on a focal level are meaningful. Dominance category and the experience of an adult female in the environment might be possible explanations for these differences in DJL and sinuosity. However, given the small sample size, those trends might also stem from different movement preferences of those particular orangutans.

When looking at possible correlations for the five selected mothers, I detected opposing trends regarding the effects of food availability on their DJL and sinuosity (Section 4.2.4). hFAI seemed to matter more family-wise with Cissy, Lilly, and Lisa (who all belong to one matriline), showing negative trends for DJL. In contrast, hFAI showed positive trends for Friska and Ellie (who belong to another matriline). However, not all relationships were significant (Figure C.4b). The pairing hFAI and sinuosity showed the inverse situation but again not for all five focals on a significant level (Figure C.7b).

Regarding the older females in the area (Cissy, Friska, and Lisa), non-fruit eFAI was significantly negatively correlated with DJL. In contrast, for the younger adult females (Ellie and Lilly), it was positively correlated, but not on a significant level for Lilly (Figure C.4d). I found the same result for the correlation between non-fruit eFAI and the sinuosity but negatively related for the younger adult females and positively for the older adult females (Figure C.7d). Hence, a more experienced non-fruit diet could lead to longer DJLs but straighter movements in younger adult females and shorter travel distances but more tortuous movements in older, more dominant adult females. This suggests opposing strategies of these females. Whereas old females seem to stay put when more non-fruit items are available, young females seem to travel more, which may suggest that they actively search for these items.

For fruit eFAI, correlations with DJL were less clear (Figure C.4c), whereas fruit eFAI was negatively correlated with the sinuosity index for all five females (Figure C.7c). These trends suggest that those five adult females move straighter but not necessarily further when experiencing more fruit. Again, this behavior may be explained by the high availability of fruit in Suaq in general and by the fact that they often need to carry, or are accompanied by, a dependent immature (Van Noordwijk et al., 2009) which restricts their movement range. When they experience more fruit, they can move more goal-oriented to these locations and do not have to search for those items.

Concluding, correlations of non-fruit eFAI with DJL and sinuosity could be interpreted as being related to the experience and age or dominance of the adult females, whereas the correlation of hFAI with the movement parameters could be more related to the females' matriline.

Chapter 5

Conclusion

5.1 Major findings

This thesis established a new way of representing food availability and investigated the effects of food availability on spatial movement patterns of the orangutans at the research site Suaq Balimbing in Sumatra. The major findings are summarized here regarding the two main themes of this thesis.

5.1.1 Fruit and Food Availability in Suaq

Allocation of feeding points and bootstrapping method

- By adding many feeding points from the *behavioral data* to the *waypoint GPS data* (Section 3.2.3), I could show that this allocation process is required to validate and complement the collected data and to improve the eFAI calculation. From gaining insight into both data sets, I conclude that neither one can replace the other as they both contribute different information on the behavior of orangutans (**RQ A.1**) (Section 3.3.1).
- At most feeding points that were present in the *behavioral data* but not in the *waypoint GPS data*, the recorded feeding time was below 30 minutes (Section 3.2.3). This indicates that researchers often miss taking GPS points on these short feeding points. However, fewer points were missing in the waypoint GPS data in recent years. This result may mean that the collecting process was optimized, as fewer feeding points needed to be added (**RQ A.1**).
- By comparing the coordinates of the *waypoint GPS data* and *behavioral data*, I could confirm that the locations of the feeding points are accurate, with an average deviation of around 11 meters (Section 2.5). Good accuracy in the GPS points helped to obtain appropriate estimates of movement parameters in Chapter 4, and it confirms to researchers that they are setting and using the GPS points accurately (**RQ A.1**) (Section 3.3.1).
- Based on the bootstrapping resampling method, I discovered that a minimum number of 10 follows per month was needed to achieve an appropriate balance between the independence of the data from a small number of individuals and days as well as the loss of too much data (**RQ A.2**) (Section 3.2.2). A cutoff size of 10 follows per month is large enough to ensure that the monthly eFAI value is calculated using follows of several individuals (Section 3.3.3).

Food availability in space and time

- I assessed the variation in the abundance of fruit-bearing trees on a temporal scale (**RQ A.3**). Monthly hFAI values varied between around 4% and 11% (Section 3.2.5). This result suggests that the Sumatran orangutans at Suaq do not face any fruit scarcity, and it probably explains why there is less temporal variation in the time spent feeding on fruit in Suaq than in other study areas, for example, Tuanan or Gunung Palung (Section 3.3.4).

- Furthermore, I assessed the variation in the food availability with space and time (**RQ A.3**). For the newly established experienced food availability (eFAI), I retrieved an average monthly value of 0.84 ±0.17 (Section 3.2.5). Looking at monthly and yearly eFAI values, I observed a significant difference for 2011 and 2021, which may relate to varying food consumption, but none for the different months (Section 3.3.4).

- eFAI, fruit eFAI, non-fruit eFAI, and 30-minute eFAI differed if analyzed separately for the different age-sex classes (**RQ A.3**) (Section 3.2.6). A possible reason for significant differences in the values of these (sub-)indices may be different foraging strategies between age-sex classes (Section 3.3.4):
  - I detected, on average, the lowest eFAI, fruit eFAI, and non-fruit eFAI values but the highest 30-minute eFAI values for flanged males. This result suggests that flanged males spend extended time exploiting one resource rather than switching quickly between resources. Movement may be energetically more costly for them than for other age-sex classes owing to their big body size.
  - For independent immatures, I detected the highest eFAI, fruit eFAI, and non-fruit eFAI values but no difference in the 30-minute eFAI compared to the other age-sex classes. Independent immatures are most likely less competent at locating big food patches, and thus they end up switching between food patches faster than other individuals. In doing so, they try to ensure sufficient energy intake to support their growing bodies.
  - I identified low 30-minute eFAI values for adult females. Together with their differing diet composition compared to the other age-sex classes (**RQ A.2**) (Section 3.2.4), this suggests that adult females get a broad and balanced diet from different food items found at various feeding places. Female orangutans need to maintain lactation and pregnancy by consuming nutrient- and protein-rich food found, for example, in young leaves (Section 3.3.2).
  - For unflanged males, I discovered no meaningful trends.

- Over three-year research periods, mean eFAI values in the grid cells of the research area are higher in the center, the South, and the North but slightly lower in the East and along the Krueng Lembang river in the West (**RQ A.3**) (Section 3.2.7). I observed a similar distribution for the fruit eFAI values but a more even distribution of values for the non-fruit eFAI. These trends could be related to the research area's layout, where fruit availability patterns vary strongly between the three forest types (peat, dry, and riverine). However, non-fruit vegetation can be found throughout the whole research area (Section 3.3.6). Local differences, however, may relate to the concept of hexagonal grid cells with an arbitrary origin, different corresponding sample sizes, or the concept of three-year research periods.

Relation of eFAI and eFAI versions to hFAI

- Between the hFAI and eFAI values, I observed a significant negative correlation (**RQ A.4**) (Section 3.2.5), whereas I had originally predicted a positive correlation, as the orangutans can only experience the food that is available in the habitat. Nevertheless, a negative relationship might indicate that with more available fruit in the habitat, maintaining a positive energy budget is easier, and food is consumed at fewer locations.
- However, I detected no correlation between the hFAI and the fruit eFAI values (**RQ A.4**). This lack of correlation means that the availability of fruit in the habitat (hFAI) does not predict the experienced fruit availability (fruit eFAI) of orangutans in Suaq (Section 3.3.5). A comparison of fruit eFAI and non-fruit eFAI showed no significant correlation but a negative trend, which may indicate that when orangutans experience less fruit, they compensate by eating non-fruit items more often.

5.1.2 Movement analysis

- All of the movement parameters significantly differed between the age-sex classes confirming the separation on an age-sex class level chosen for the linear mixed-effects models (**RQ B.1**). Generally, I observed larger DJLs for the Suaq orangutans compared to other study sites. Individuals at Suaq can maintain a high energy intake because of the abundance of fruit in their environment. However, contradicting effects of fruit eFAI and non-fruit eFAI on the DJLs of orangutans showed that an overall eFAI is less suitable when predicting ranging behavior (**RQ B.2**) (Section 4.1.3). Instead, fruit eFAI and non-fruit eFAI values were used separately besides hFAI values as fixed effects in the linear mixed-effects models.
- hFAI could not explain any variation in the movement parameters of the orangutans, as expected based on the findings of previous studies (**RQ B.2**), most likely due to generally high fruit availability in the habitat throughout the whole year, which is in line with previous findings of Graf (2021) (Section 4.3.2).
- Contrary to the findings for hFAI, fruit eFAI and non-fruit eFAI showed some significant effects on the movement parameters DJL and sinuosity in the overall, female, male, and age-sex class models (Sections 4.2.2 and 4.3.2) confirming the prediction for **RQ B.2**:
  - Non-fruit eFAI had a negative effect on DJL but a positive effect on the sinuosity of flanged males. Thus, when flanged males consume more non-fruit items, they may travel shorter distances because they feed longer at the same location rather than switching quickly between resources which would be in line with the findings about the 30-minute eFAI (Section 3.2.6).
  - An age-sex class comparison indicates that adult females move the shortest but most tortuous distances (Section 4.2.1). Carrying their young offspring or moving after independently moving but still dependent offspring may lead to higher sinuosity and likely slow them down (Section 4.3.1). However, fruit eFAI and non-fruit eFAI had a significant effect on the movement of adult females. Results suggest that adult females travel longer and straighter distances when consuming more fruit but shorter distances when focusing on non-fruit items. This behavior indicates that adult females know the

locations of fruit trees and how to travel efficiently between them. On the individual level, older adult females traveled on average shorter DJL but more tortuous than younger adult females, which may be related to increasing experience in locating food (Section 4.2.4).

- For unflanged males, I observed the longest DJL but the lowest sinuosity values of all age-sex classes (Section 4.2.1). However, I detected no significant effect of fruit eFAI or non-fruit eFAI on their DJL or sinuosity. A lack of such an effect may be related to the fact that the movement of unflanged males is more affected by their mating strategy than the foraging strategy, as there is no restriction by a changing fruit availability in Suaq.
- Results for independent immatures suggest that their daily movement is not defined by either fruit or non-fruit diet. Social factors likely play a larger role in what way and how far independent immatures move, as they are more gregarious and social than adult orangutans.

In conclusion, the single most crucial insight produced by this work is that eFAI offered a differentiated view of food availability and its effects on the movement behavior of orangutans in Suaq. However, fine-grained differences in the behavior of different age-sex classes were recorded only by further dividing eFAI into a fruit and non-fruit eFAI part.

5.2 Limitations

The results and conclusions of this thesis are limited to the study area and the individuals therein. This study area in Suaq on Sumatra has a high fruit availability year-round compared to many other orangutan research sites, especially on Borneo, which make certain inferences about the experienced fruit or non-fruit availability not simply transferable to other study sites. Furthermore, I used an arbitrary, human-defined concept of 'month' because the data was collected that way. However, animals do not follow this concept regarding their behavior. By the same token, the representation of animal movement by a sampling interval of 30 minutes is only a coarse approximation of the actual traveled distance. The results of this thesis may therefore change depending on the time frame used for calculating the new eFAI values but also depending on the sampling interval that affects the movement parameters. Moreover, the movement of orangutans represented by the day journey length was only calculated horizontally, while orangutans move in three dimensions.

Further, the spatial and temporal representation of the eFAI value in hexagonal grid cells (Section 3.2.7) is limited due to the lack of sufficient focal follows based on which the eFAI values were calculated. I calculated eFAI values for research periods of three years, which is suitable for Suaq as fruit availability does not change drastically. But to discover changing ranging behaviors based on annual fruit cycles at other research sites, those periods would be too long.

In the analysis, it was evident that the *waypoint GPS data* was biased towards flanged males and adult females, and fewer numbers of follows were available for unflanged males and independent immatures (Section 2.5). Those smaller sample sizes may be less representative of the age-sex classes. Furthermore, the restriction of a minimum number of follows per month based on the bootstrapping resampling method increased the possibility that the respective calculated eFAI value is independent of a small number of individuals and days. Nevertheless, this process discarded many months of data that could have been used to infer orangutan behavior (Section 3.2.2). This difference was visible between the full and reduced models in Chapter 4. I conclude that if in the future more than 10 nest-to-nest follow days were available for all the months, the conclusions drawn in this thesis about the effects of food availability on movement parameters could be validated.

Finally, in light of the eFAI introduction and analysis, it has to be mentioned that this new representation of food availability is also limited because it does not include the quality and quantity of the food consumed at a specific location. This information would be required to make appropriate assumptions about the energy budget of an orangutan and the consequent potential to roam in the environment.

5.3 Future work

Several possible avenues exist for future research to build upon this thesis. First, the introduction and calculation of the new eFAI and the versions of fruit eFAI and non-fruit eFAI proved useful in explaining some of the variations of the movement of the orangutans at the Suaq research site. However, further studies on other orangutan populations are necessary to confirm their use besides the already established hFAI. I argue that the approach in this thesis needs to be tested at other locations with high fruit availability for comparison purposes. Applying the concepts to environments that feature fruit scarcity and mast-fruiting events during certain times of the year and where the food availability in the habitat already had a significant effect on the movement of orangutans, such as Tuanan on Borneo, is needed as well. The effects of fruit eFAI and non-fruit eFAI may be more pronounced there because of a greater variation in fruit availability. Furthermore, studies on other apes might also benefit from this new approach.

Second, as the introduced representation of food availability does not include the quality and quantity of food, adding an additional term to the eFAI calculation that includes the calorie content from the different food items may prove useful to the analysis of ranging behavior. In order to be applied in practice, however, such an extended index would also require the necessary data.

Third, as no effects of fruit eFAI and non-fruit eFAI on movement parameters were discovered for the age-sex class independent immatures, the analysis could be repeated with two groups split into female and male independent immatures as it was done, for example, in Vogel et al. (2017). This would shed further light on the effect of fruit or non-fruit eFAI on their ranging behavior. However, a clear interpretation would be difficult because of the currently small sample sizes.

Fourth, many studies in the past have focused on the home ranges of orangutans and their determinants over extended periods of time. Preliminary results in my analysis – not included in this thesis – suggested no effect of eFAI on the home ranges of females. However, testing the effect of fruit eFAI and non-fruit eFAI separately on home ranges for the most-tracked females, which was beyond the scope of this thesis, might prove helpful in understanding their ranging behavior.

Fifth, focusing on the sinuosity and straightness between feeding trees and not only between standardized 30-minute GPS points may lead to a better understanding of whether orangutans head straight to feeding hotspots or instead visit many trees on the way.

Last but not least, for future work with the data for Suaq orangutans, I strongly recommend adding missing feeding points (or other information) from the *behavioral data* to improve and complement the *waypoint GPS data*. In that way, as much accurate information as possible can be obtained.

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Appendix A

Data preparation

A.1 Data overview

TABLE A.1: Example of the first 25 lines of follow number 2978 in the *behavioral data*.

followNr	focalID	activityFocal	itemFocal	jenisFocal	dateDay	dateMonth	dateYear	timeHour	timeMin	classFocal	sexFocal	observer1
2978	friska	M	NA	NA	4	6	2020	6	20	Mother	Female	fikar
2978	friska	M	NA	NA	4	6	2020	6	22	Mother	Female	fikar
2978	friska	F	Fr/M	ABSG	4	6	2020	6	24	Mother	Female	fikar
2978	friska	F	Fr/M	ABSG	4	6	2020	6	26	Mother	Female	fikar
2978	friska	F	Fr/M	ABSG	4	6	2020	6	28	Mother	Female	fikar
2978	friska	F	Fr/M	ABSG	4	6	2020	6	30	Mother	Female	fikar
2978	friska	F	Fr/M	ABSG	4	6	2020	6	32	Mother	Female	fikar
2978	friska	F	Fr/M	ABSG	4	6	2020	6	34	Mother	Female	fikar
2978	friska	F	Fr/M	ABSG	4	6	2020	6	36	Mother	Female	fikar
2978	friska	F	Fr/M	ABSG	4	6	2020	6	38	Mother	Female	fikar
2978	friska	F	Fr/M	ABSG	4	6	2020	6	40	Mother	Female	fikar
2978	friska	R	NA	NA	4	6	2020	6	42	Mother	Female	fikar
2978	friska	R	NA	NA	4	6	2020	6	44	Mother	Female	fikar
2978	friska	R	NA	NA	4	6	2020	6	46	Mother	Female	fikar
2978	friska	R	NA	NA	4	6	2020	6	48	Mother	Female	fikar
2978	friska	R	NA	NA	4	6	2020	6	50	Mother	Female	fikar
2978	friska	M	NA	NA	4	6	2020	6	52	Mother	Female	fikar
2978	friska	M	NA	NA	4	6	2020	6	54	Mother	Female	fikar
2978	friska	M	NA	NA	4	6	2020	6	56	Mother	Female	fikar
2978	friska	M	NA	NA	4	6	2020	6	58	Mother	Female	fikar
2978	friska	M	NA	NA	4	6	2020	7	0	Mother	Female	fikar
2978	friska	R	NA	NA	4	6	2020	7	2	Mother	Female	fikar
2978	friska	M	NA	NA	4	6	2020	7	4	Mother	Female	fikar
2978	friska	M	NA	NA	4	6	2020	7	6	Mother	Female	fikar
2978	friska	M	NA	NA	4	6	2020	7	8	Mother	Female	fikar

TABLE A.2: Example of all follows in June 2020 listed in the *follow log data*. The follow number 2978 is highlighted in bold typeface because the other exemplary tables refer to this focal follow.

followNR	dateDay	dateMonth	dateYear	focalName	classFocal	sexFocal	observer1	observer2	lengthActivity
2976	3	6	2020	friska	Mother	Female	saidi	adami	393
2977	3	6	2020	frankie	Infant	Male	adami	saidi	393
2978	**4**	**6**	**2020**	**friska**	**Mother**	**Female**	**fikar**	**saidi**	**714**
2979	4	6	2020	frankie	Infant	Male	saidi	fikar	721
2980	5	6	2020	friska	Mother	Female	fikar	adami	633
2981	5	6	2020	frankie	Infant	Male	adami	fikar	642
2982	10	6	2020	friska	Mother	Female	ulil	armas	40
2983	10	6	2020	frankie	Infant	Female	armas	ulil	47
2984	11	6	2020	friska	Mother	Female	armas	ulil	707
2985	11	6	2020	frankie	Infant	Male	ulil	armas	700
2986	12	6	2020	friska	Mother	Female	saidi	ulil	636
2987	12	6	2020	frankie	Infant	Male	ulil	saidi	636
2988	13	6	2020	friska	Mother	Female	armas	saidi	589
2989	13	6	2020	frankie	Infant	Male	saidi	armas	603
2990	22	6	2020	ellie	Mother	Female	fikar	ulil	107
2991	22	6	2020	eden	Infant	Female	ulil	fikar	107
2992	22	6	2020	rakus	Unfl.Male	Male	saidi	armas	411
2993	23	6	2020	ellie	Mother	Female	adami	ulil	676
2994	23	6	2020	eden	Infant	Female	ulil	adami	675
2995	29	6	2020	fl.male	Fl.Male	Male	saidi	armas	410
2996	30	6	2020	fl.male	Fl.Male	Male	ulil	armas	434

TABLE A.3: Example of follow number 2978 in the *waypoint GPS data*.

UniqueID	**FollowNumber**	**FollowType**	**FocalName**	**PointActivity**	**Symbol**	**PtType**	**Day**	**Month**	**Year**	**Hour**	**Minute**	**classFocal**	**sexFocal**	**Observer**	**UTME**	**UTMN**	**GPXFileName**
44340	2978	NN	friska	sp	Circle, Green	mornnest	4	6	2020	06	20	adult female	female	fikar	324772.7389	337265.7245	20200604_Friska_Fikar_NN_2978
44341	2978	NN	friska	f fr absg	Flag, Green	tree	4	6	2020	06	24	adult female	female	fikar	324773.8516	337268.3829	20200604_Friska_Fikar_NN_2978
44342	2978	NN	friska	f fr absg	Flag, Red	range	4	6	2020	06	30	adult female	female	fikar	324773.0671	337267.1606	20200604_Friska_Fikar_NN_2978
44343	2978	NN	friska	m	Flag, Red	range	4	6	2020	07	00	adult female	female	fikar	324755.4344	337289.7456	20200604_Friska_Fikar_NN_2978
44344	2978	NN	friska	f fr strpd	Flag, Green	tree	4	6	2020	07	28	adult female	female	fikar	324669.293	337377.2257	20200604_Friska_Fikar_NN_2978
44345	2978	NN	friska	f fr strpd	Flag, Red	range	4	6	2020	07	30	adult female	female	fikar	324666.8502	337376.1264	20200604_Friska_Fikar_NN_2978
44346	2978	NN	friska	f fr strpd	Flag, Red	range	4	6	2020	08	00	adult female	female	fikar	324669.402	337375.3441	20200604_Friska_Fikar_NN_2978
44347	2978	NN	friska	f fr strpd	Flag, Red	range	4	6	2020	08	30	adult female	female	fikar	324668.0734	337377.8948	20200604_Friska_Fikar_NN_2978
44348	2978	NN	friska	f fl rbgb	Flag, Green	tree	4	6	2020	08	44	adult female	female	fikar	324664.3068	337382.655	20200604_Friska_Fikar_NN_2978
44349	2978	NN	friska	f fl rbgb	Flag, Red	range	4	6	2020	09	00	adult female	female	fikar	324664.3068	337382.655	20200604_Friska_Fikar_NN_2978
44350	2978	NN	friska	f fr kulbt	Flag, Green	tree	4	6	2020	09	20	adult female	female	fikar	324697.4435	337391.7821	20200604_Friska_Fikar_NN_2978
44351	2978	NN	friska	f fr kulbt	Flag, Red	range	4	6	2020	09	30	adult female	female	fikar	324697.6596	337386.6934	20200604_Friska_Fikar_NN_2978
44352	2978	NN	friska	m	Flag, Red	range	4	6	2020	10	00	adult female	female	fikar	324707.1805	337436.5245	20200604_Friska_Fikar_NN_2978
44353	2978	NN	friska	f veg apd	Flag, Green	tree	4	6	2020	10	02	adult female	female	fikar	324708.2792	337448.6829	20200604_Friska_Fikar_NN_2978
44354	2978	NN	friska	f fr kulbt	Flag, Green	tree	4	6	2020	10	14	adult female	female	fikar	324715.5601	337464.1874	20200604_Friska_Fikar_NN_2978
44355	2978	NN	friska	r	Flag, Red	range	4	6	2020	10	30	adult female	female	fikar	324740.2263	337459.9434	20200604_Friska_Fikar_NN_2978
44356	2978	NN	friska	f veg atb	Flag, Green	tree	4	6	2020	10	36	adult female	female	fikar	324760.3785	337478.1632	20200604_Friska_Fikar_NN_2978
44357	2978	NN	friska	f veg atb	Flag, Red	range	4	6	2020	11	00	adult female	female	fikar	324745.6954	337472.5403	20200604_Friska_Fikar_NN_2978
44358	2978	NN	friska	f fr absg	Flag, Green	tree	4	6	2020	11	02	adult female	female	fikar	324757.919	337471.9756	20200604_Friska_Fikar_NN_2978
44359	2978	NN	friska	f fr absg	Flag, Red	range	4	6	2020	11	30	adult female	female	fikar	324760.3785	337478.1632	20200604_Friska_Fikar_NN_2978
44360	2978	NN	friska	f fr absg	Flag, Red	range	4	6	2020	12	00	adult female	female	fikar	324724.7601	337447.6949	20200604_Friska_Fikar_NN_2978
44361	2978	NN	friska	r	Flag, Red	range	4	6	2020	12	30	adult female	female	fikar	324804.0244	337454.9841	20200604_Friska_Fikar_NN_2978
44362	2978	NN	friska	f ins rayap	Flag, Green	tree	4	6	2020	12	54	adult female	female	fikar	324756.0269	337471.5335	20200604_Friska_Fikar_NN_2978
44363	2978	NN	friska	f ins rayap	Flag, Red	range	4	6	2020	13	00	adult female	female	fikar	324759.2501	337471.0839	20200604_Friska_Fikar_NN_2978
44364	2978	NN	friska	f ins rayap	Flag, Red	range	4	6	2020	13	30	adult female	female	fikar	324761.142	337471.4148	20200604_Friska_Fikar_NN_2978
44365	2978	NN	friska	f ins rayap	Flag, Red	range	4	6	2020	14	00	adult female	female	fikar	324756.0269	337471.5335	20200604_Friska_Fikar_NN_2978
44366	2978	NN	friska	m	Flag, Red	range	4	6	2020	14	30	adult female	female	fikar	324749.9681	337507.9205	20200604_Friska_Fikar_NN_2978
44367	2978	NN	friska	f fr knds	Flag, Green	tree	4	6	2020	14	34	adult female	female	fikar	324754.8309	337551.8545	20200604_Friska_Fikar_NN_2978
44368	2978	NN	friska	f fr merangan	Flag, Green	tree	4	6	2020	14	46	adult female	female	fikar	324750.78	337604.1245	20200604_Friska_Fikar_NN_2978
44369	2978	NN	friska	f fr merangan	Flag, Red	range	4	6	2020	15	00	adult female	female	fikar	324747.7746	337600.5884	20200604_Friska_Fikar_NN_2978
44370	2978	NN	friska	m	Flag, Red	range	4	6	2020	15	30	adult female	female	fikar	324733.1481	337633.5587	20200604_Friska_Fikar_NN_2978
44371	2978	NN	friska	r	Flag, Red	range	4	6	2020	16	00	adult female	female	fikar	324735.0151	337693.1605	20200604_Friska_Fikar_NN_2978
44372	2978	NN	friska	m	Flag, Red	range	4	6	2020	16	30	adult female	female	fikar	324798.5226	337718.8241	20200604_Friska_Fikar_NN_2978
44373	2978	NN	friska	f ins rayap	Flag, Green	tree	4	6	2020	16	32	adult female	female	fikar	324769.0264	337720.582	20200604_Friska_Fikar_NN_2978
44374	2978	NN	friska	m	Flag, Red	range	4	6	2020	17	00	adult female	female	fikar	324831.1582	337761.2436	20200604_Friska_Fikar_NN_2978
44375	2978	NN	friska	f fr ur	Flag, Green	tree	4	6	2020	17	16	adult female	female	fikar	324792.3408	337868.3218	20200604_Friska_Fikar_NN_2978
44376	2978	NN	friska	m	Flag, Red	range	4	6	2020	17	30	adult female	female	fikar	324760.2097	337896.6929	20200604_Friska_Fikar_NN_2978
44377	2978	NN	friska	m	Flag, Red	range	4	6	2020	18	00	adult female	female	fikar	324668.5561	337935.5227	20200604_Friska_Fikar_NN_2978
44378	2978	NN	friska	sm	Circle, Green	nightnest	4	6	2020	18	10	adult female	female	fikar	324658.5981	337962.4062	20200604_Friska_Fikar_NN_2978

TABLE A.4: Example of the first 20 lines of follow number 2978 in the *track GPS data*.

followNR	**followtype**	**orangutanname**	**day**	**month**	**year**	**datetime**	**UTME**	**UTMN**	**fileN**
2978	NN	friska	4	6	2020	2020-06-04 06:01:18	324773.380993105	337271.555243962	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 06:06:46	324776.107560345	337269.215634352	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 06:11:46	324768.99736476	337268.51238821	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 06:16:46	324766.582157692	337267.14421481	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 06:21:46	324772.616457982	337264.84610179	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 06:26:46	324751.827607017	337263.643866337	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 06:31:46	324775.998399096	337271.023116158	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 06:36:46	324759.306136135	337267.729508274	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 06:41:46	324763.377852484	337267.742080697	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 06:46:46	324765.786308086	337270.861976027	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 06:51:46	324772.495476816	337271.30629641	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 06:56:46	324764.202260801	337270.799418072	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 07:01:46	324745.195380805	337290.281461646	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 07:06:46	324774.52845653	337310.693668633	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 07:07:47	324762.822101497	337282.711228446	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 07:12:47	324740.439611264	337351.209090208	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 07:17:47	324730.074345747	337354.607215806	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 07:22:47	324711.830097245	337360.4081164	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 07:27:47	324665.520048422	337358.59452835	20200604_Friska_Fikar_NN_2978
2978	NN	friska	4	6	2020	2020-06-04 07:32:47	324671.920774624	337377.446180197	20200604_Friska_Fikar_NN_2978

A.2 Data cleaning

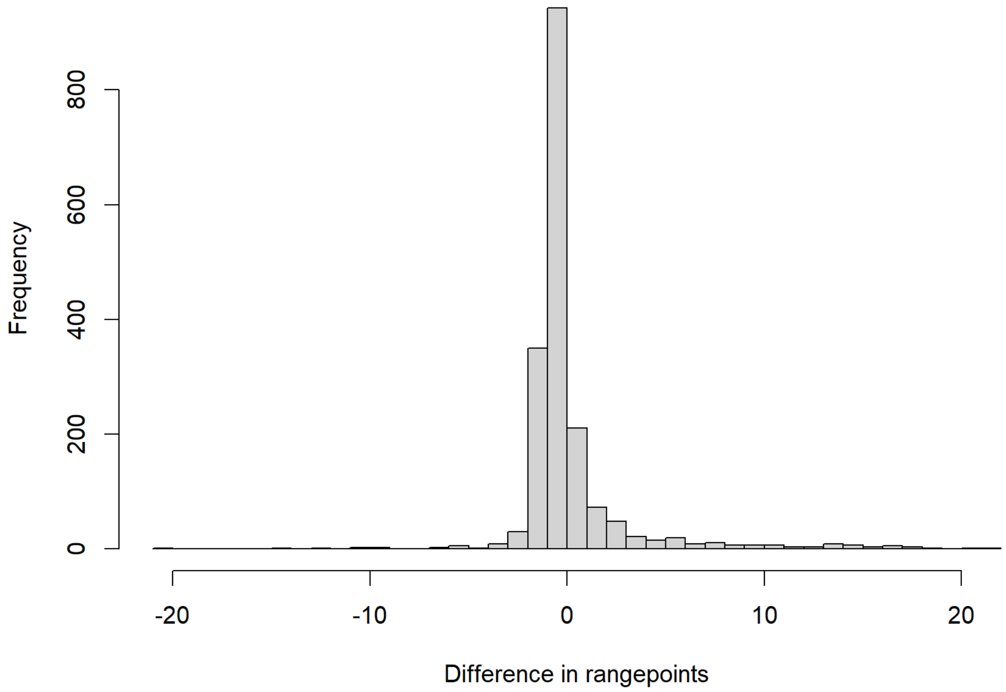


FIGURE A.1: Histogram of range points difference between the *behavioral data* and the *waypoint GPS data*, which were filtered for +4 and -2 range points.

A.3 Used R packages

TABLE A.5: Overview of the main R packages used in this thesis.

R package	Version	Usage	Purpose	Citation
dplyr	1.0.7	P/eFAI, MA	data wrangling	Wickham et al. (2022)
tidyr	1.1.4	P/eFAI, MA	data wrangling	Wickham and Girlich (2022)
tidyverse	1.3.1	P/eFAI, MA	data wrangling	Wickham et al. (2019)
lubridate	1.8.0	P/eFAI, MA	handling times and dates	Grolemund Garrett and Wickham (2011)
sf	1.0-5	P/eFAI, MA	import, geometric operations	Pebesma (2018)
ggplot2	3.3.5	P/eFAI, MA	plots	Wickham (2016)
rgdal	1.5-28	P/eFAI, MA	handling spatial reference systems	Bivand et al. (2022)
viridis	0.6.2	P/eFAI, MA	color visualization	Garnier et al. (2021)
gridExtra	2.3	P/eFAI	plots ordering	Auguie (2017)
trajr	1.4.0	MA	trajectories, sinuosity, straightness	McLean and Skowron Volponi (2018)
adehabitatLT	0.3.25	MA	space and habitat use	Calenge (2006)
GGally	2.1.2	MA	overview scatterplots	Schloerke et al. (2021)
ggfortify	0.4.14	MA	diagnostics	Tang et al. (2016)
lme4	1.1-27.1	MA	generalized linear mixed effects	Bates et al. (2015)
lmerTest	3.1-3	MA	p-values of linear mixed models	Kuznetsova et al. (2017)

P/eFAI: data processing and eFAI calculation, MA: movement analysis

A.4 Activity duration

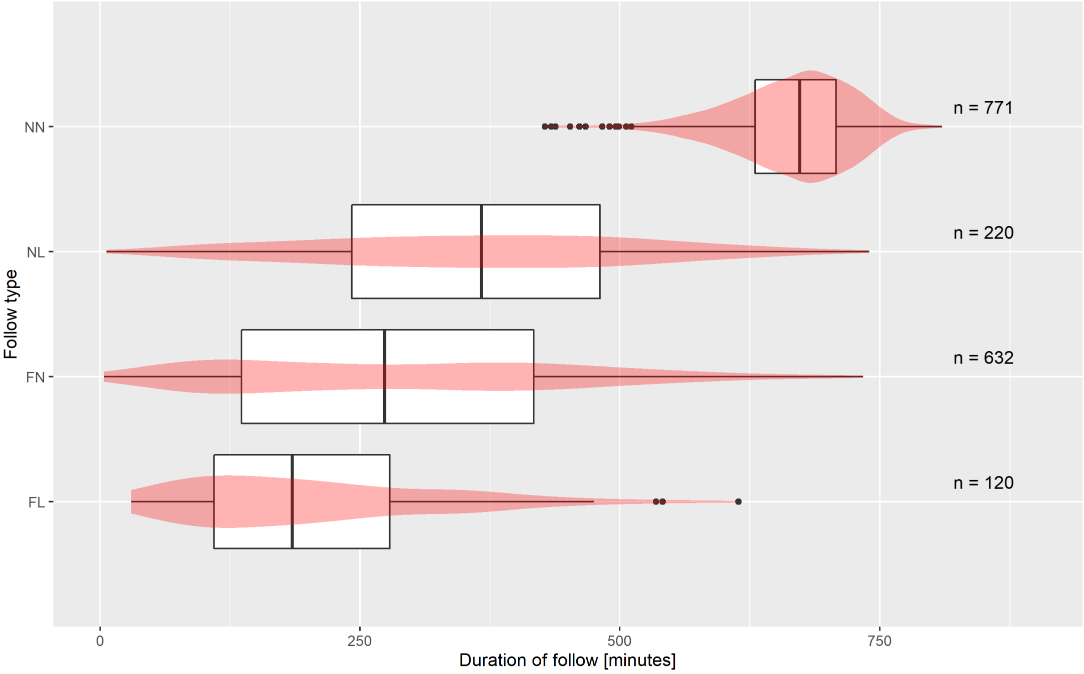


FIGURE A.2: Box plot of the different follow types nest-to-nest (NN), nest-to-lost (NL), found-to-nest (FN), and found-to-lost (FL) and the corresponding activity duration. The overlaid violin plot shows the density distribution.

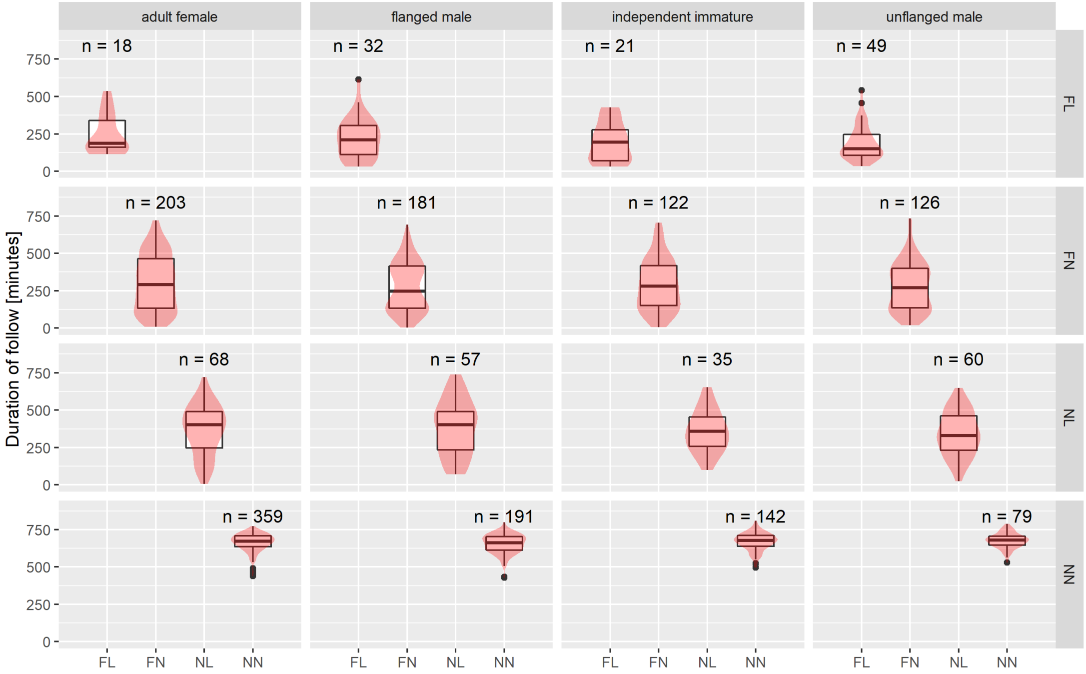


FIGURE A.3: Box plot of the different follow types nest-to-nest (NN), nest-to-lost (NL), found-to-nest (FN), and found-to-lost (FL) per age-sex class and the observed activity duration. The overlaid violin plot shows the density distribution.

A.5 Behavioral data and waypoint GPS data comparison

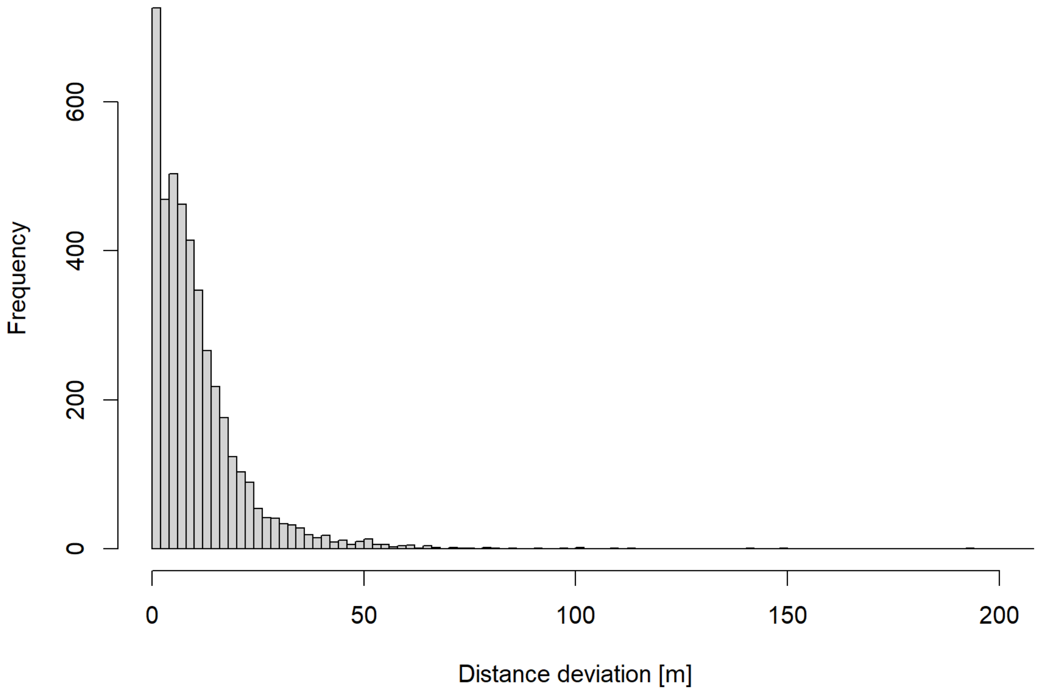


FIGURE A.4: Histogram of distance deviations between the *behavioral data* with coordinates from the *track GPS data* and the *waypoint GPS data*. Manually and automatically taken GPS coordinates of feeding trees were compared. The distribution is right-skewed, indicating that many follows have a low distance deviation. Only 7 feeding trees had a distance deviation greater than 100 m.

Appendix B

Fruit and Food Availability

B.1 Correlation between the number of range points and feeding points

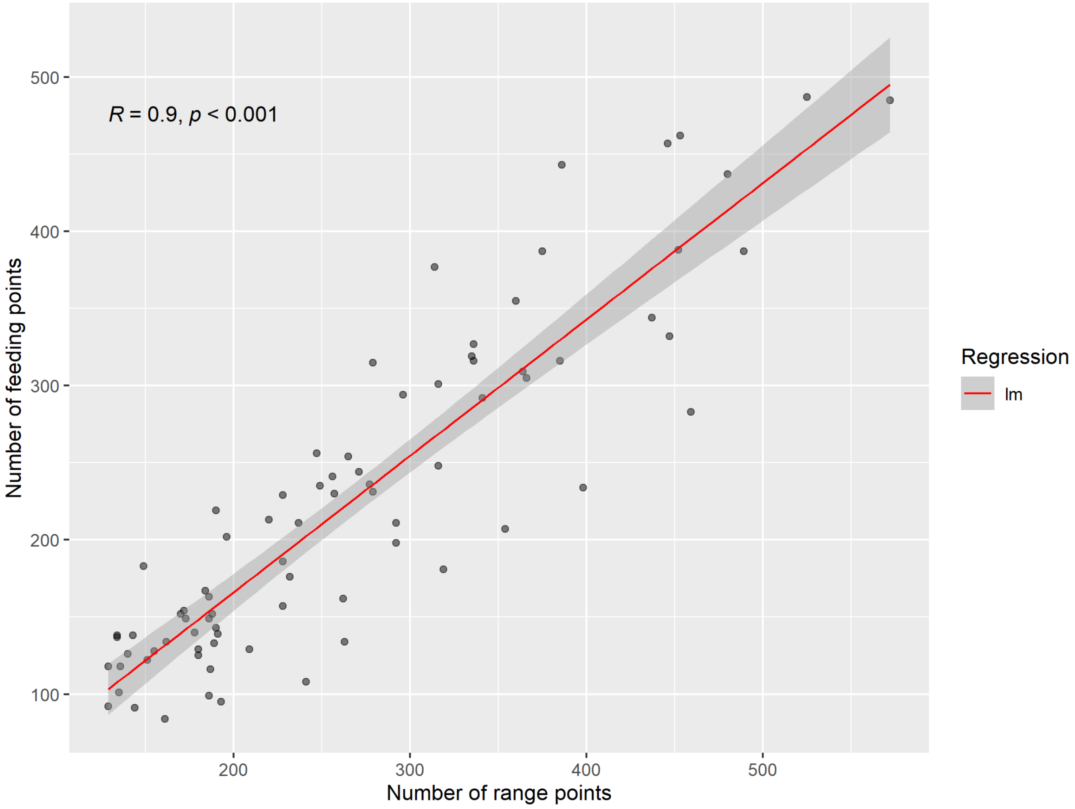


FIGURE B.1: Positive correlation between the number of range points and the number of feeding points on a monthly basis. Pearson's correlation coefficient 0.9 suggests that the correlation is very strong with a significance level of $p < 0.001$. Overall, the ratio is 0.73.

B.2 Feeding locations in the study area

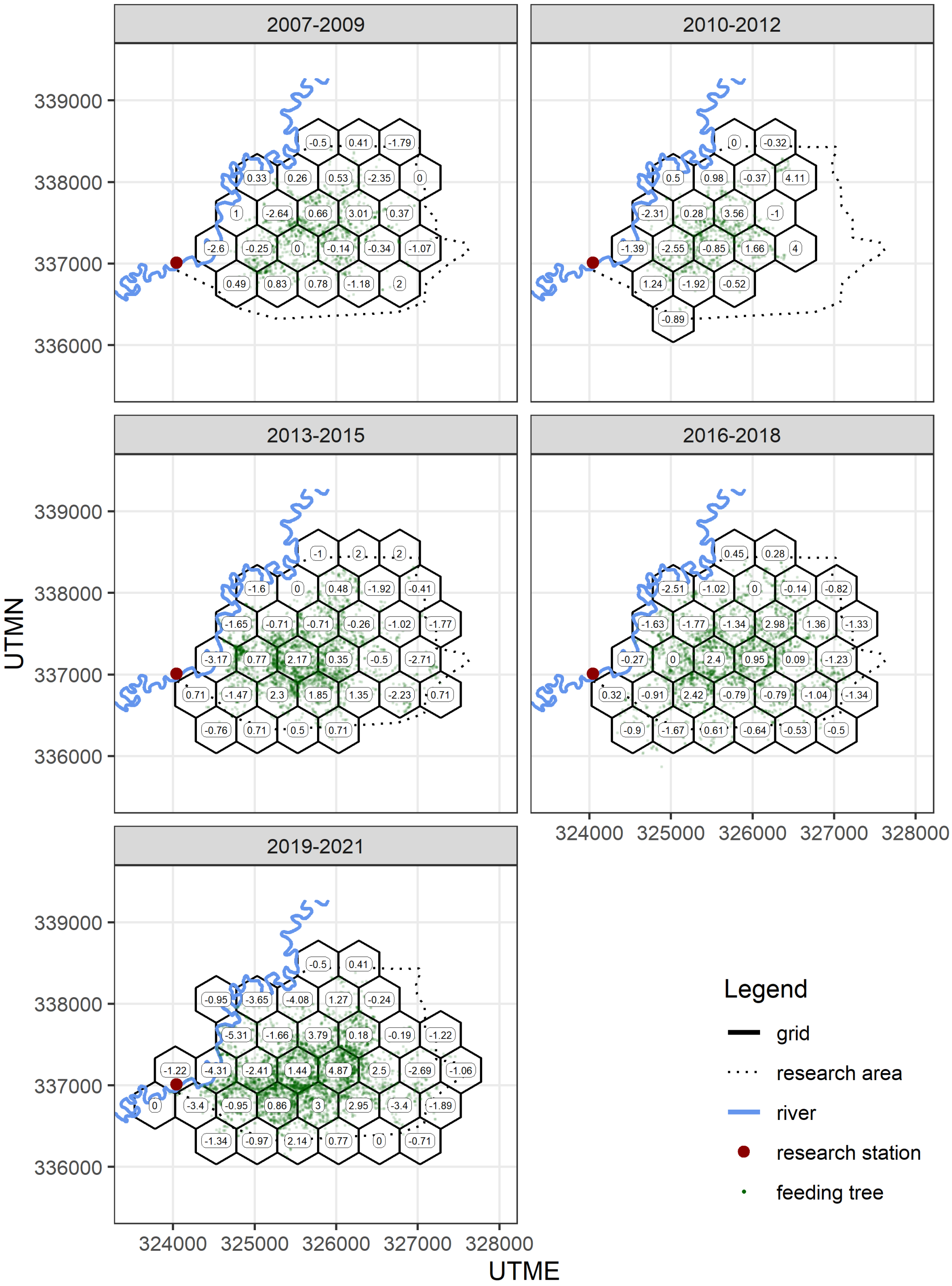


FIGURE B.2: Pearson residuals from the χ^2-test in a hexagonal grid of 500 m for research periods of three years. Positive numbers indicate that more feeding events were observed than expected assuming a uniform distribution, whereas negative numbers show fewer feeding events. Missing cells indicate no data was collected.

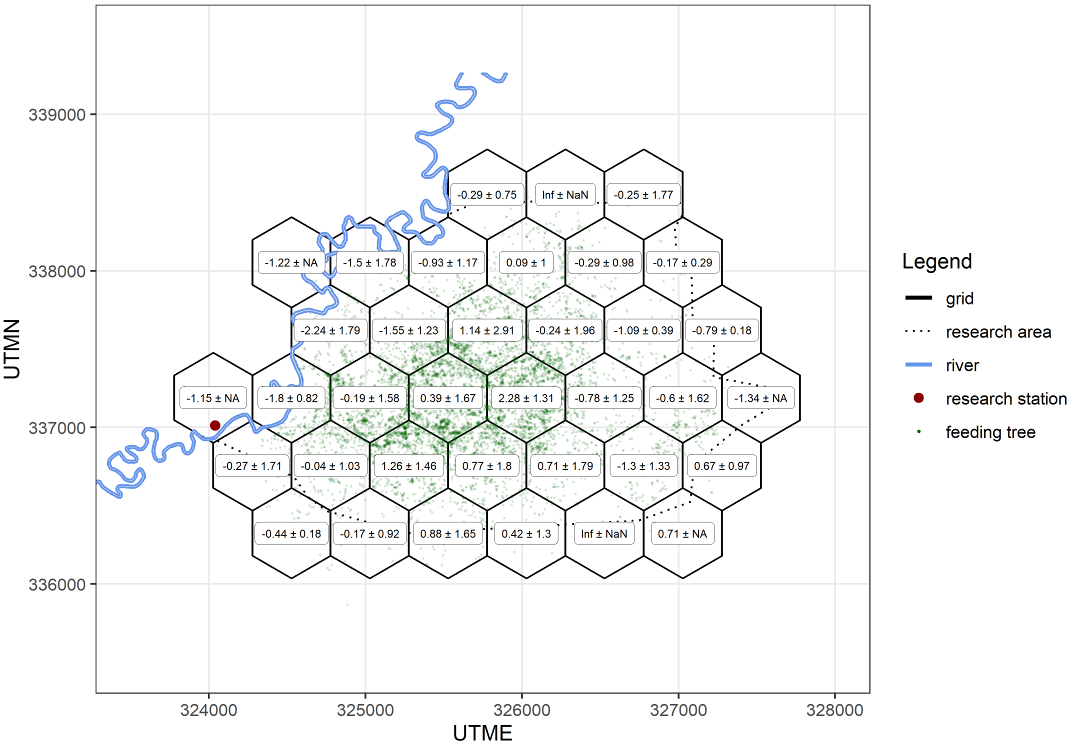


FIGURE B.3: Mean and standard deviations of the Pearson residuals of *fruit feeding points* in hexagonal grid cells of 500 m. Positive numbers indicate that more feeding events were observed than expected assuming a uniform distribution, whereas negative numbers show fewer feeding events. NA values occurred if the specific cell only contained information from one research period. In such cases, it was not possible to calculate standard deviations. Inf values occurred in a cell if during a research period Pearson residuals could not be calculated.

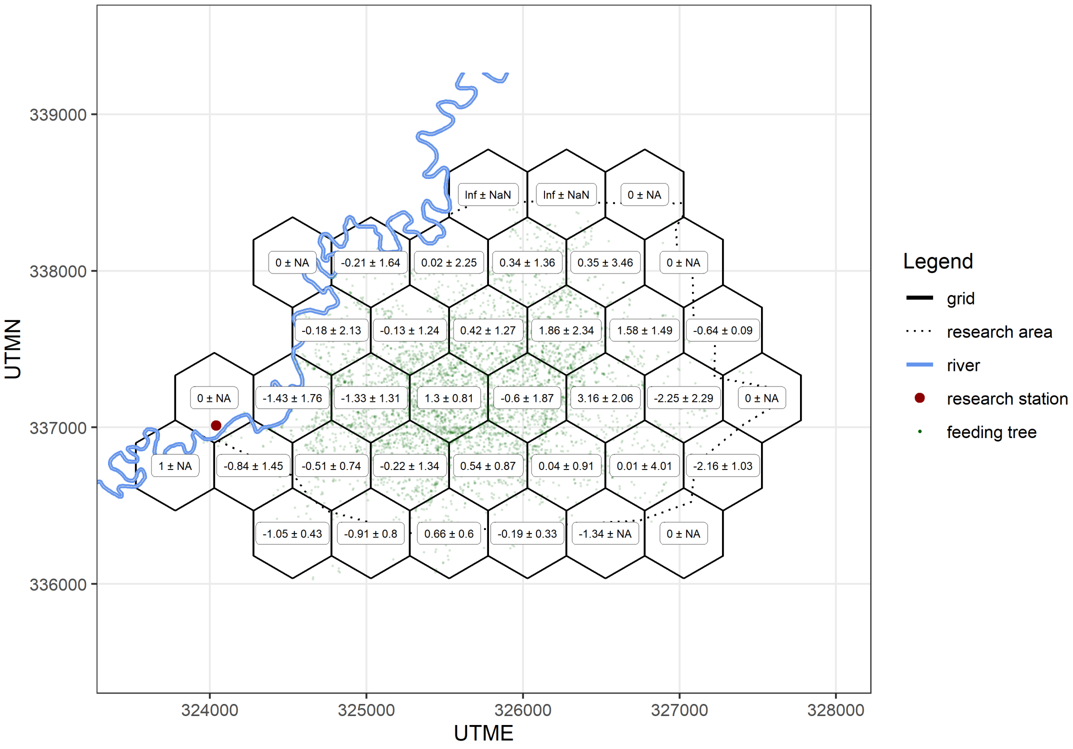


FIGURE B.4: Mean and standard deviations of the Pearson residuals of *non-fruit feeding points* in hexagonal grid cells of 500 m. Positive numbers indicate that more feeding events were observed than expected assuming a uniform distribution, whereas negative numbers show fewer feeding events. NA values occurred if the specific cell only contained information from one research period. In such cases, it was not possible to calculate standard deviations. Inf values occurred in a cell if during a research period Pearson residuals could not be calculated.

B.3 Bootstrapping

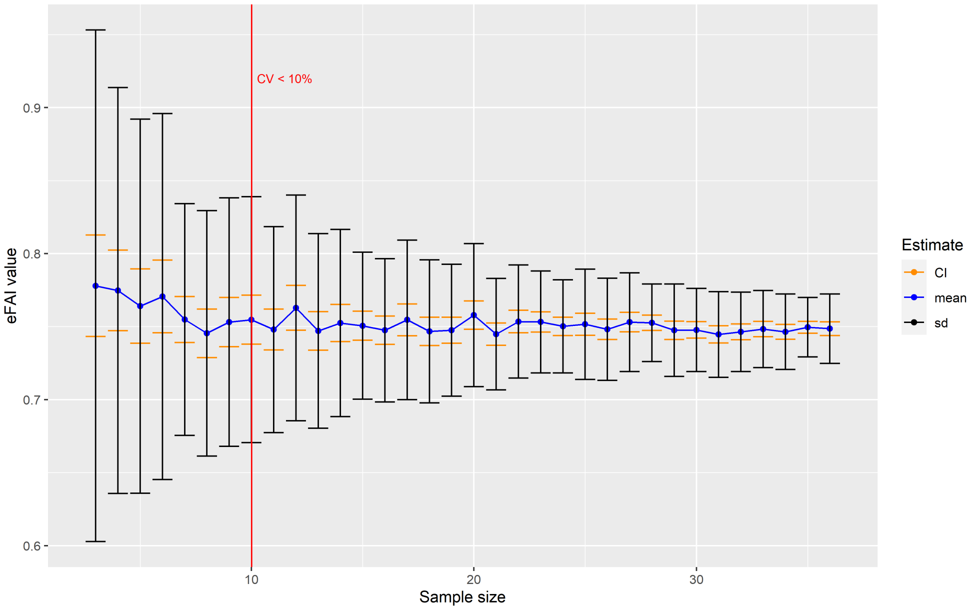


FIGURE B.5: eFAI calculation and bootstrapping resampling for the example of November 2020. For each sample size from 3 to 36 mean values are marked by a blue dot and connected with a blue line. Black error bars show the corresponding standard deviation and confidence intervals are given in orange. For a sample size of 10, a red line indicates where the CV was the first time below a threshold of 10%.

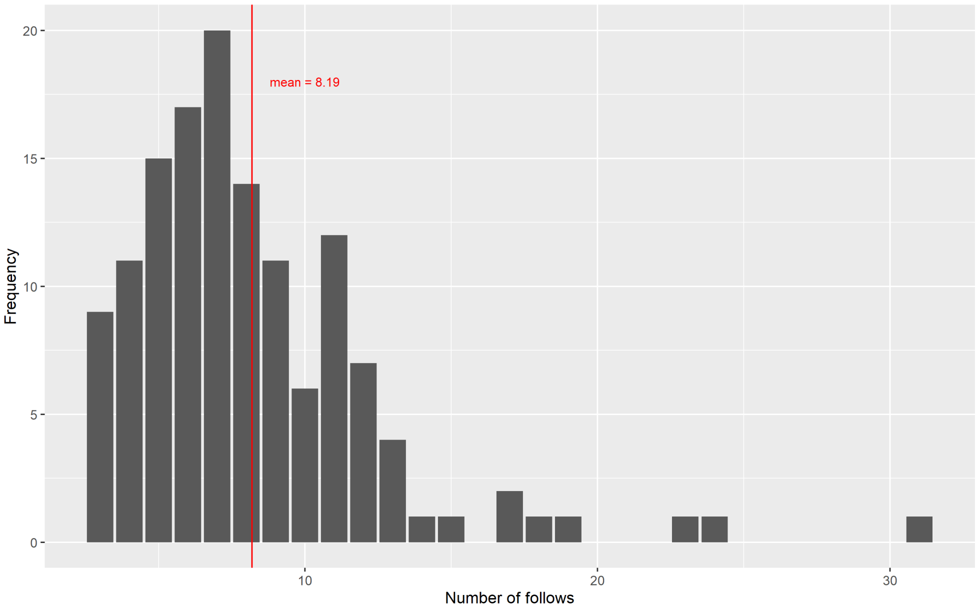


FIGURE B.6: Histogram of the minimum number of follows per month where CV is below a threshold of 10%. The red line indicates the mean of 8.19 follows.

B.4 Allocation process

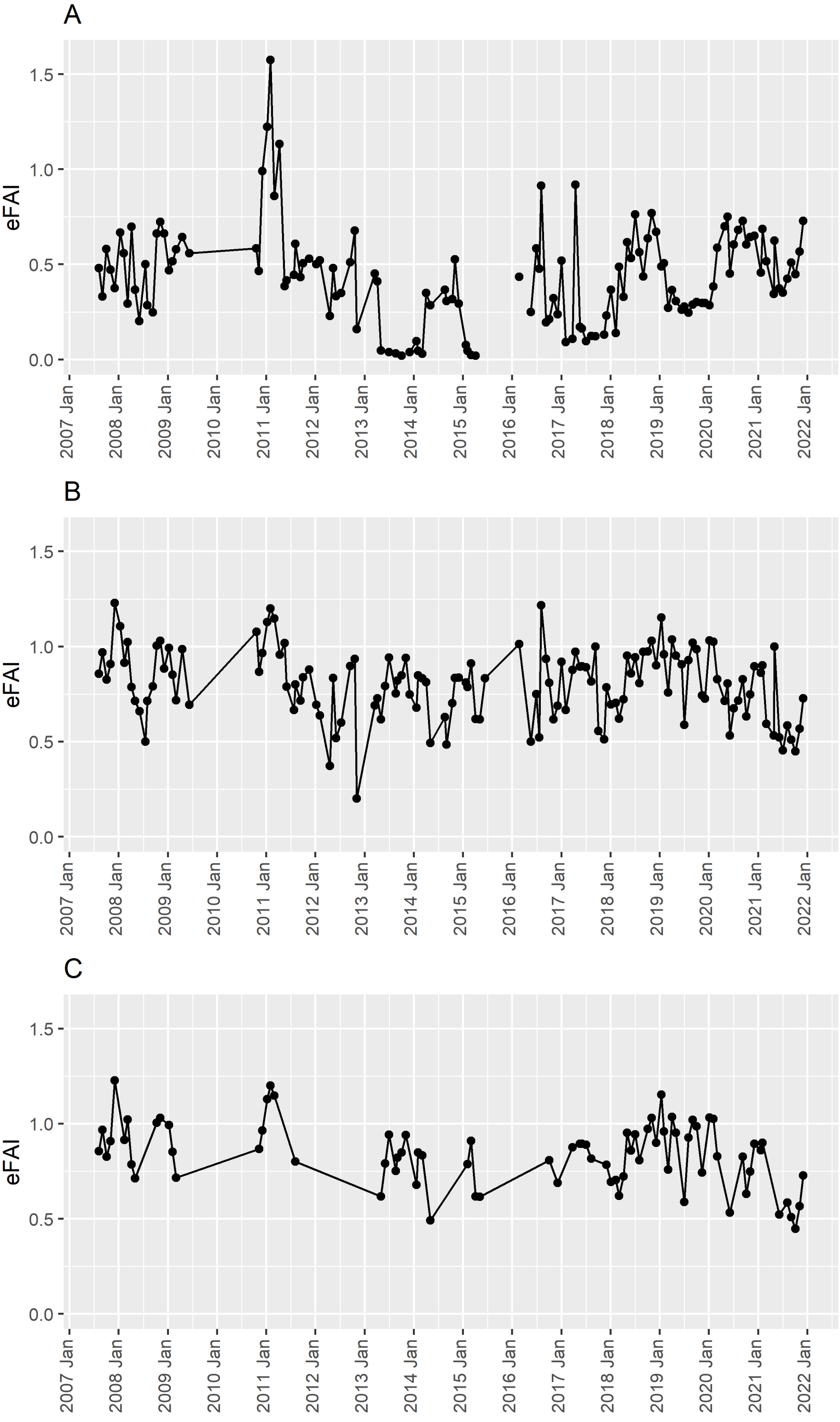


FIGURE B.7: eFAI values per month over time for the initial waypoints data (A), the waypoints data with additional feeding points from the activity data (B), and in addition for a minimum number of 10 follows per month (C).

B.5 Food overview

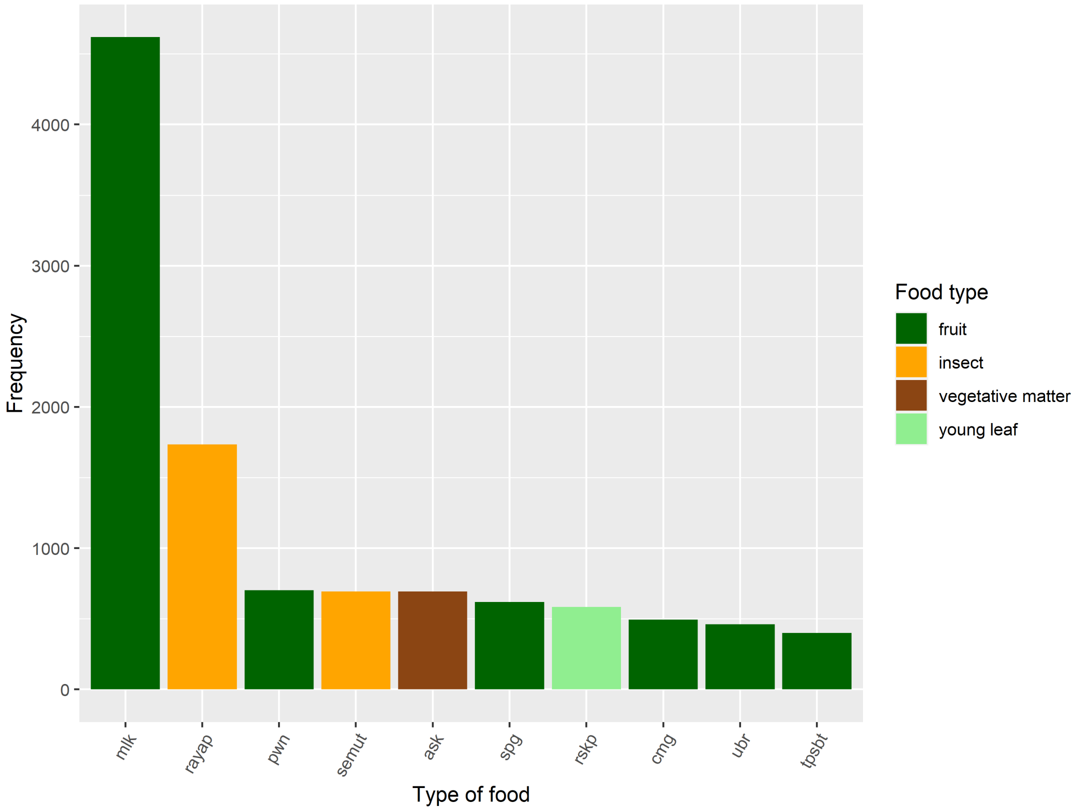


FIGURE B.8: Top 10 food items during the follows and their corresponding frequency. The most common food type is fruit, mostly the malacca fruit (*mlk*), besides young leaves and lianas (*ask*, vegetative matter). Two insect species are mainly eaten: termites (*rayap*) and ants (*semut*).

B.6 hFAI and eFAI

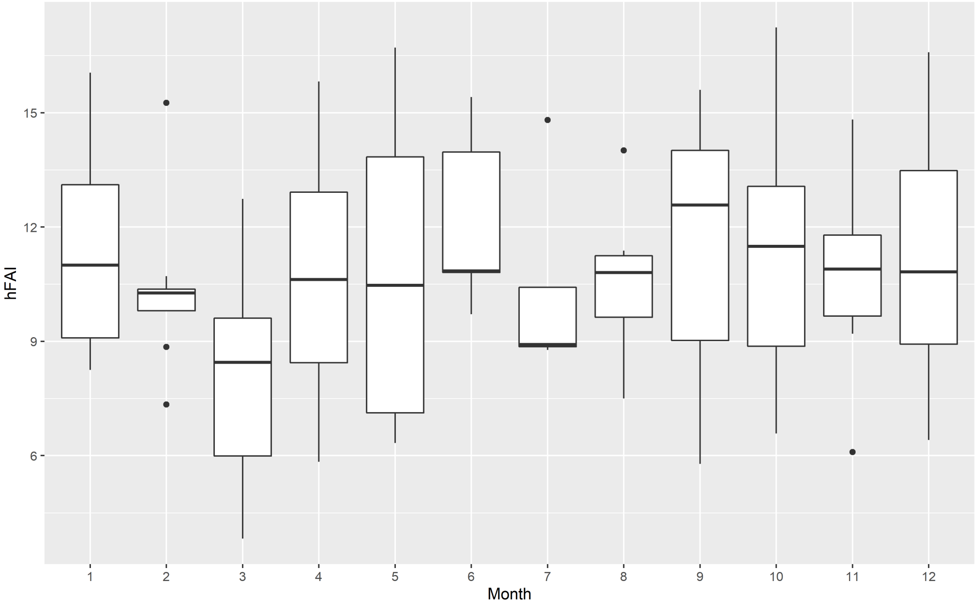


FIGURE B.9: Variation of hFAI for different months visualized in boxplots. An analysis of variance (ANOVA) suggests that there is no difference in hFAI values between months (F(1) = 1.247, p = 0.268).

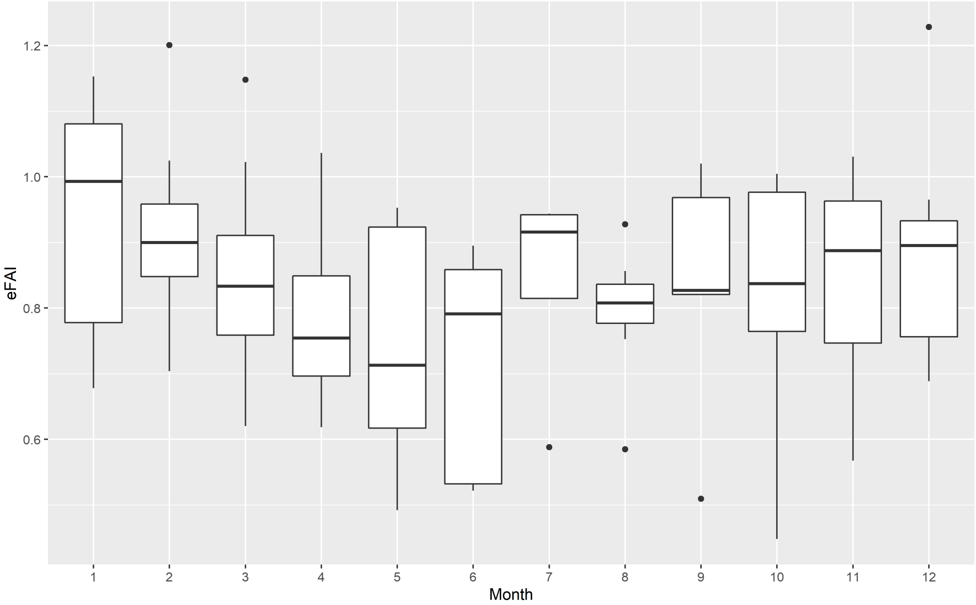


FIGURE B.10: Variation of eFAI for different months visualized in boxplots. An analysis of variance (ANOVA) suggests that there is no difference in eFAI values between months (ANOVA, F(1) = 0.618, p = 0.434).

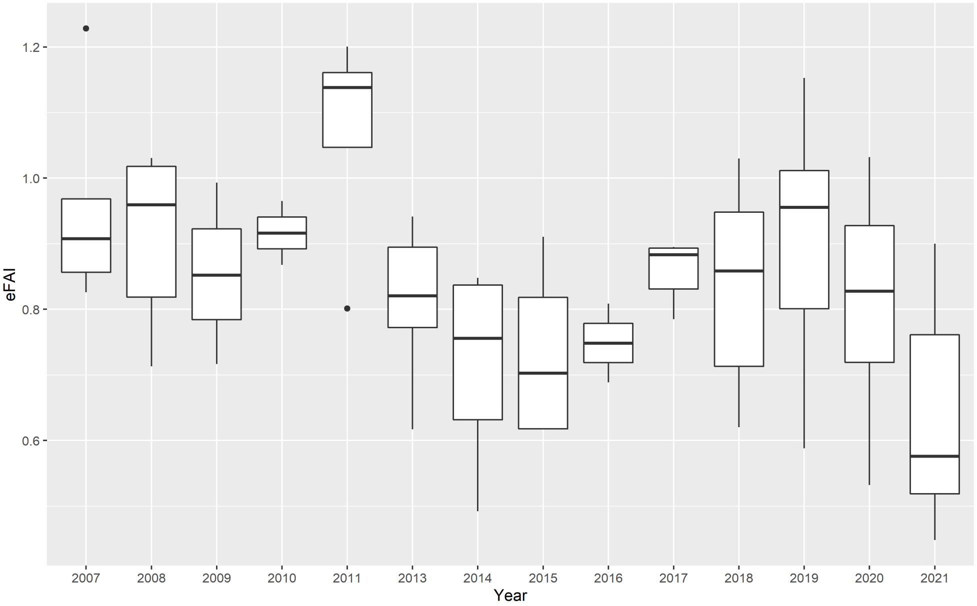


FIGURE B.11: Variation of eFAI for different years visualized in boxplots. An analysis of variance (ANOVA) of the eFAI values suggests that there is a significant difference in eFAI values between the years (ANOVA, F(1) = 8.741, p = 0.004).

B.7 Comparison of hFAI with eFAI and eFAI versions

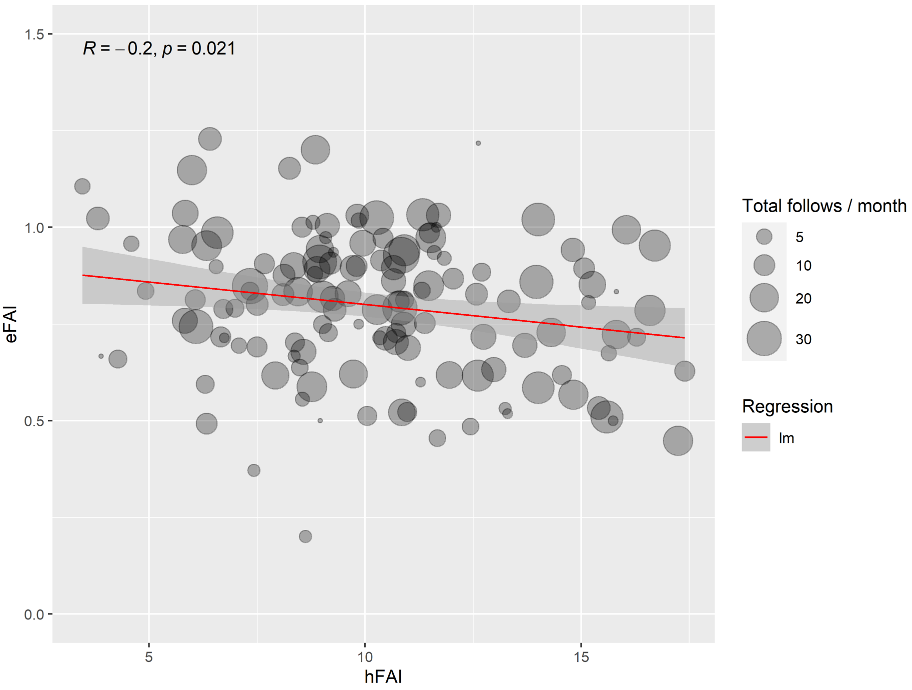


FIGURE B.12: Comparison of eFAI and hFAI values for all 140 months. The size of the point symbols is scaled proportionally to the number of follows per month.

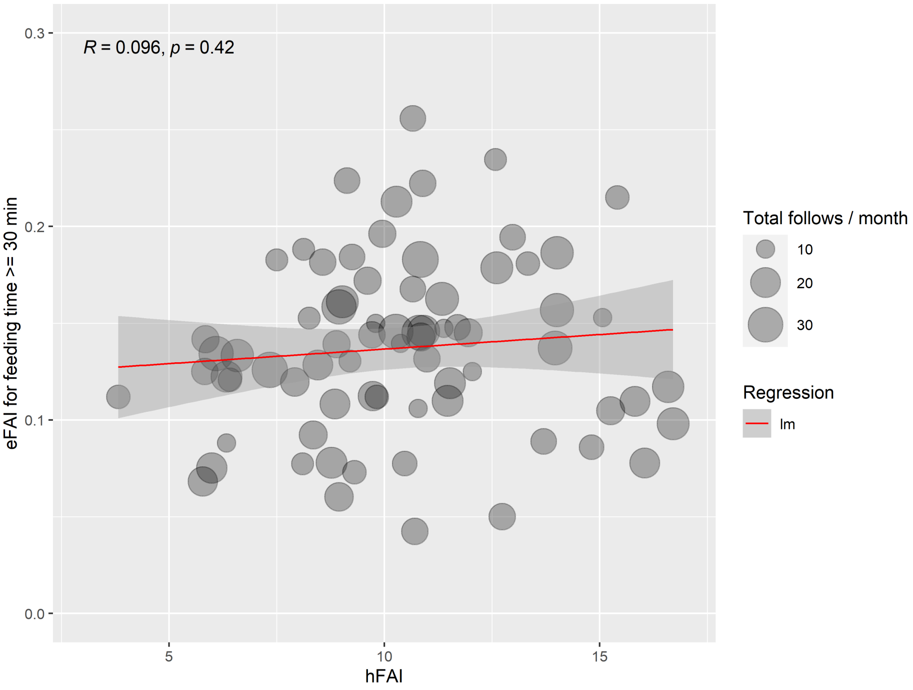


FIGURE B.13: Comparison of the 30-minute eFAI and hFAI values for those months with a minimum of 10 follows. The size of the point symbols is scaled proportionally to the number of follows per month.

B.8 Differences in eFAI and eFAI versions for different age-sex classes

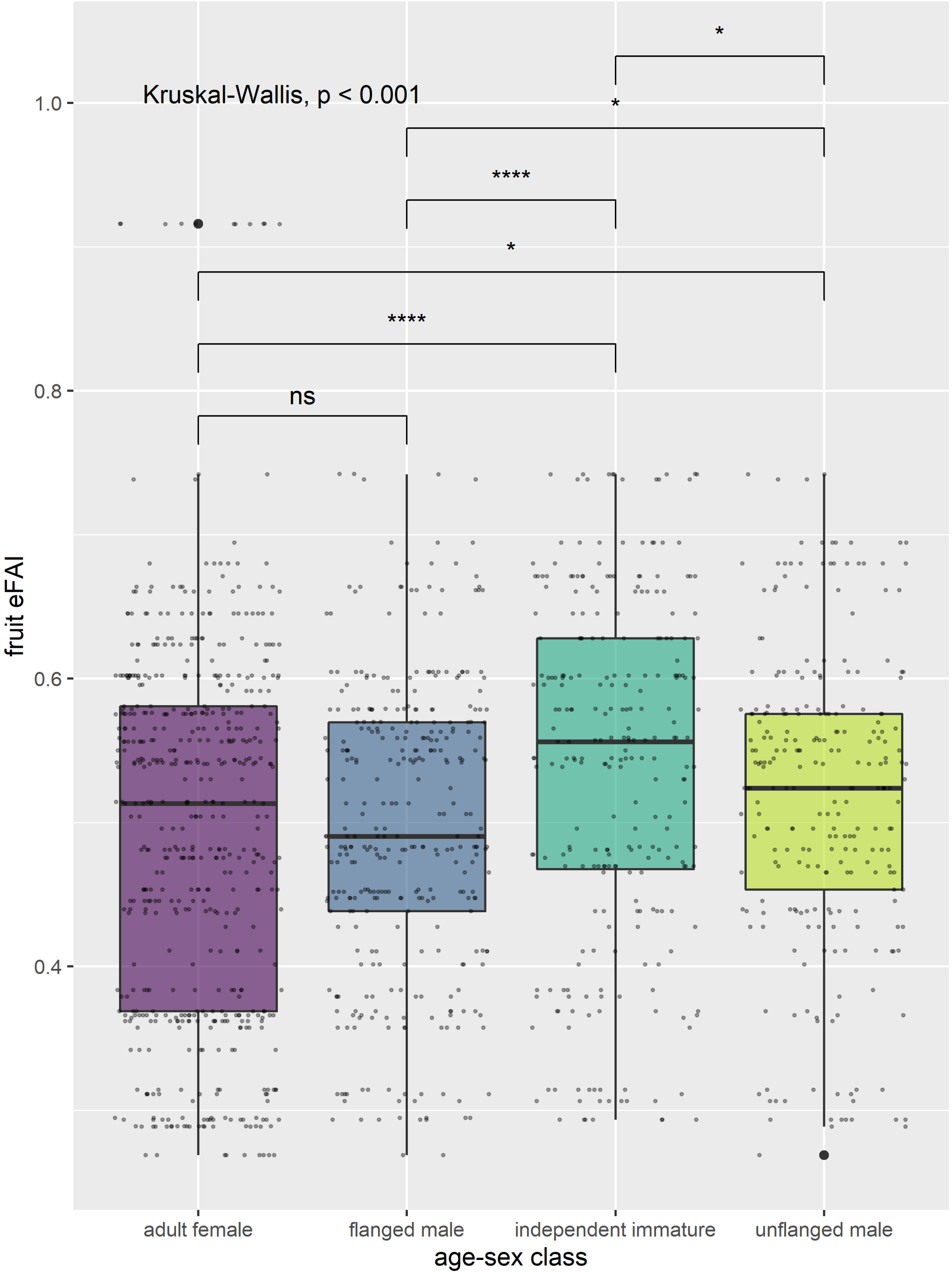


FIGURE B.14: Fruit eFAI values for different age-sex classes. Pairwise Wilcoxon signed rank (WSR) tests and overall a Kruskal-Wallis test were performed. Significance levels: $^{****}p < 0.0001$; $^{*}p < 0.05$; ns $p > 0.05$.

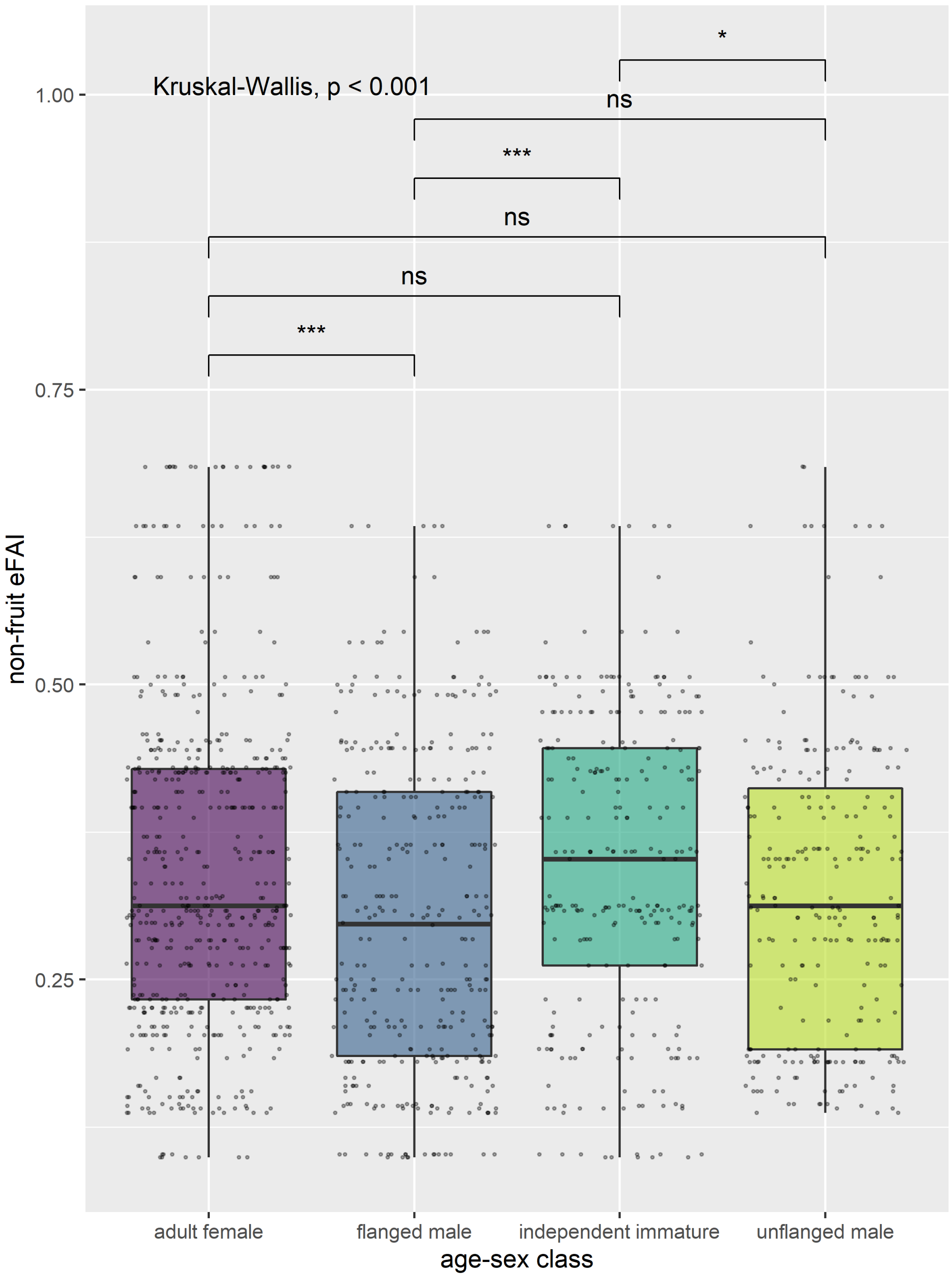


FIGURE B.15: Non-fruit eFAI values for different age-sex classes. Pairwise Wilcoxon signed rank (WSR) tests and overall a Kruskal-Wallis test were performed. Significance levels: $^{***}p < 0.001$; $^{*}p < 0.05$; ns $p > 0.05$.

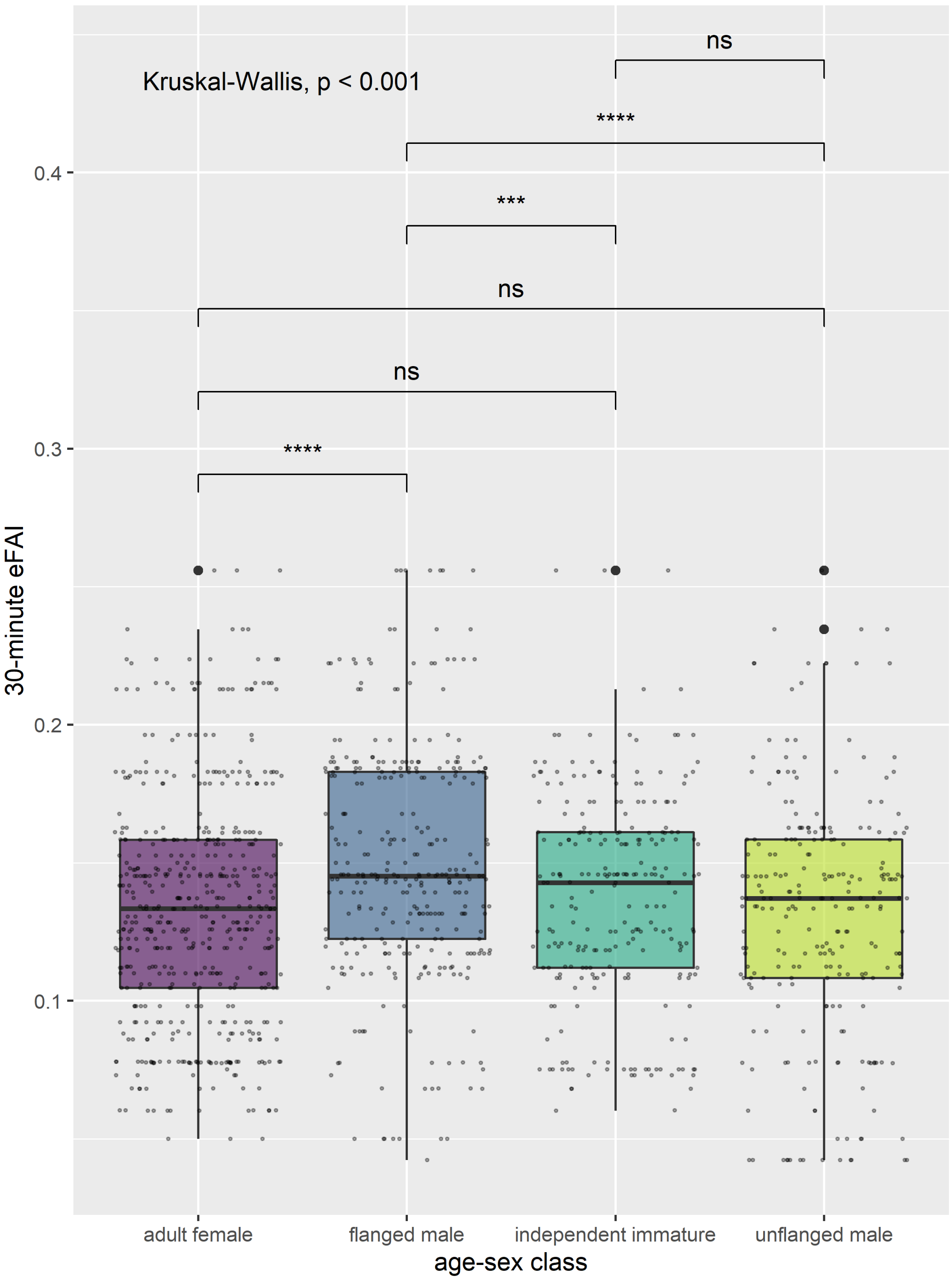


FIGURE B.16: eFAI values for feeding time >= 30 minutes and different age-sex classes. Pairwise Wilcoxon signed rank (WSR) tests and overall a Kruskal-Wallis test were performed. Significance levels: $^{****}p < 0.0001$; $^{***}p < 0.001$; ns $p > 0.05$.

B.9 eFAI variations in a hexagonal grid

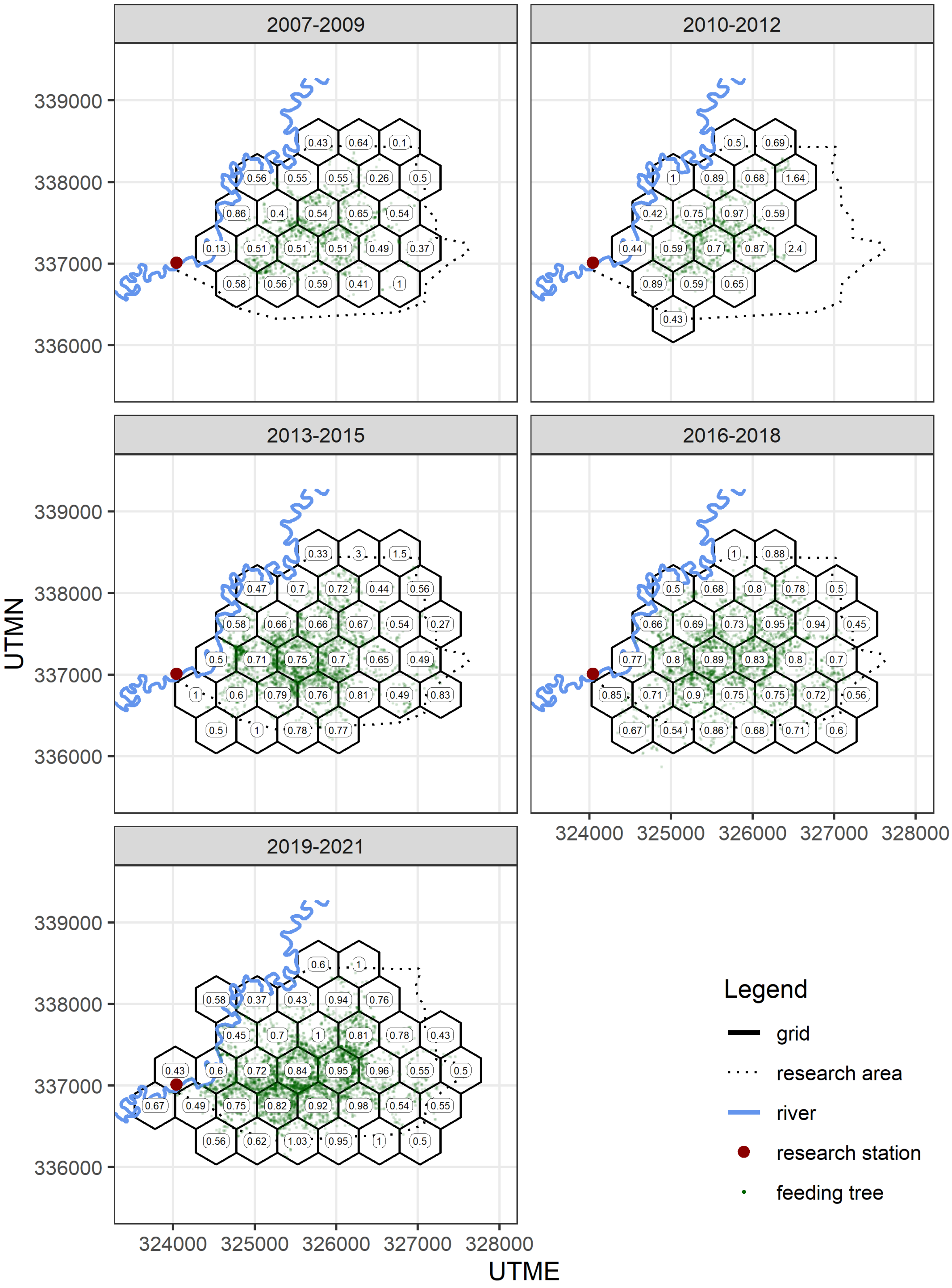


FIGURE B.17: eFAI values in a hexagonal grid of 500m for research periods of three years, respectively. Higher numbers indicate more feeding points in relation to range points. Where cells are missing no data was collected during this research period.

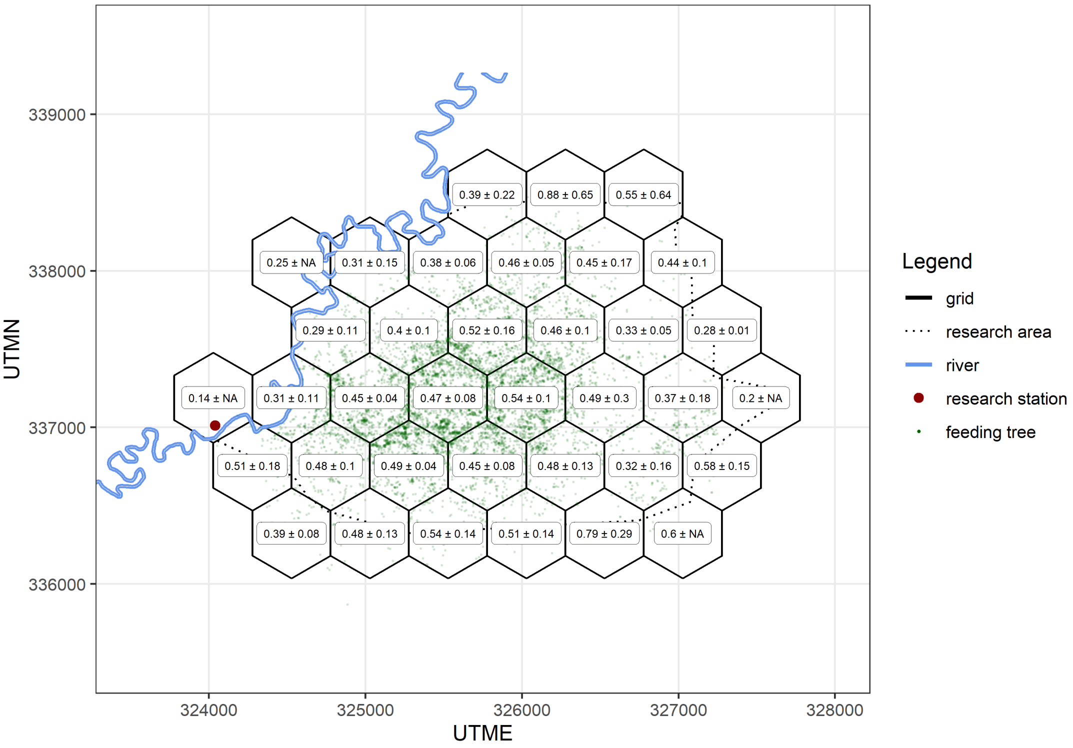


FIGURE B.18: Mean fruit eFAI values and standard deviations in hexagonal grid cells of 500 m for research periods of three years, respectively. NA values occur if the specific cell only contained information from one research period. In such cases, it was not possible to calculate standard deviations.

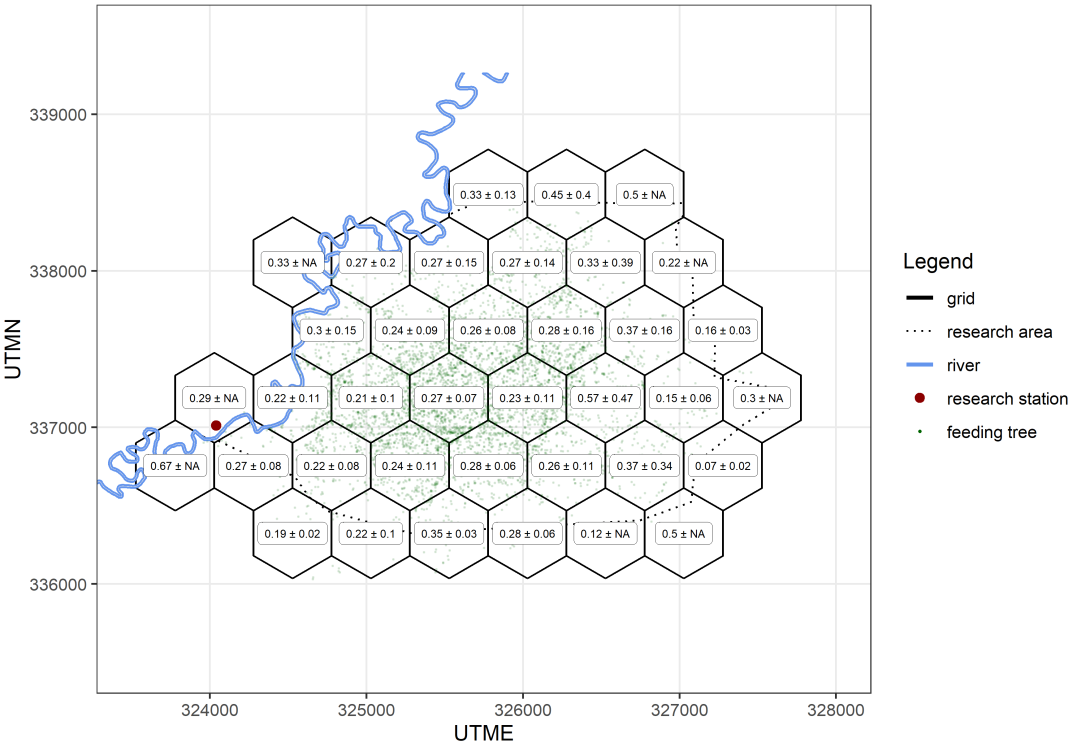


FIGURE B.19: Mean non-fruit eFAI values and standard deviations in hexagonal grid cells of 500 m for research periods of three years, respectively. NA values occur if the specific cell only contained information from one research period. In such cases, it was not possible to calculate standard deviations.

Appendix C

Movement analysis

C.1 Overview

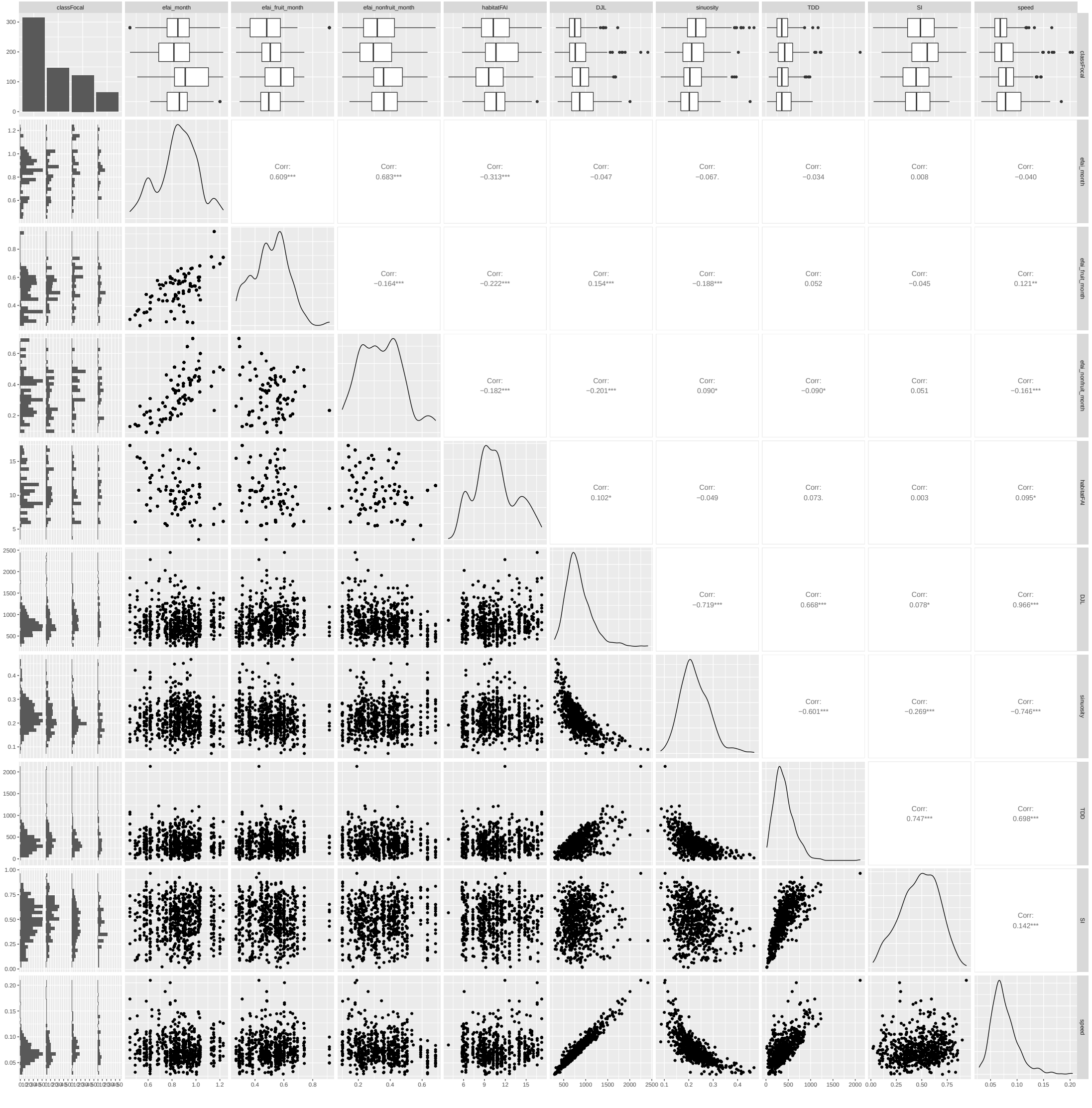


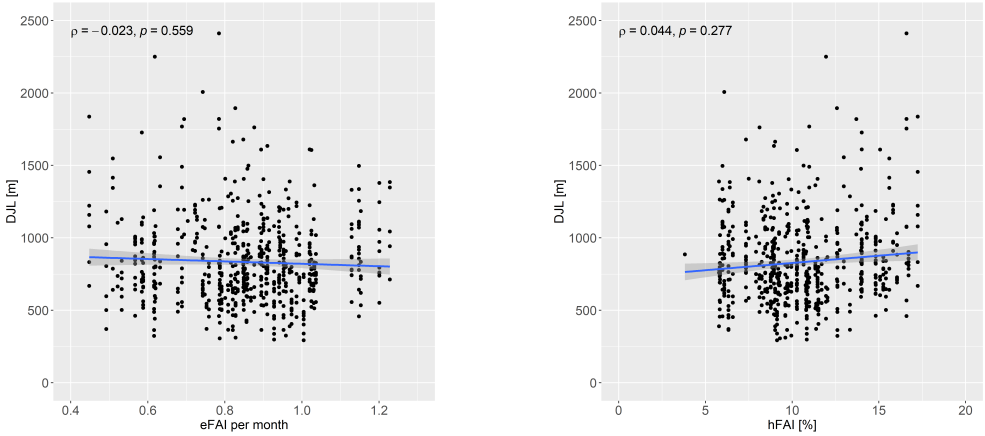
FIGURE C.1: Scatterplot matrix of movement parameters (response effects) and food availability indices (fixed effects).

C.2 Movement parameters per focal

TABLE C.1: Overview of movement parameters per focal and for nest-to-nest follows.

Focal	Class	# Follows	DJL [m]	TDD [m]	SI	Sinuosity	Speed [km/h]	Length	Trees	Points	Sampling rate
alice	adult female	4	1097±257	570±334	0.5±0.27	0.18±0.03	0.094±0.02	11:35:45	21	23.2	00:28:41
cissy	adult female	32	730±210	330±161	0.45±0.18	0.23±0.05	0.071±0.02	10:15:58	18	20.4	00:28:55
dodi	adult female	1	968±NA	424±NA	0.44±NA	0.22±NA	0.084±NA	11:35:00	16	23	00:28:58
ellie	adult female	52	798±168	408±175	0.51±0.17	0.23±0.04	0.071±0.01	11:17:43	19	22.4	00:28:54
friska	adult female	94	795±214	401±198	0.49±0.16	0.24±0.06	0.071±0.02	11:11:13	17	22	00:29:20
halte	adult female	7	704±129	202±166	0.3±0.23	0.26±0.04	0.063±0.01	11:02:34	19	20.3	00:31:16
karma	adult female	1	653±NA	556±NA	0.85±NA	0.14±NA	0.073±NA	08:56:00	26	17	00:29:47
lilly	adult female	6	935±251	490±238	0.51±0.16	0.21±0.04	0.08±0.02	11:42:50	21	23	00:29:18
lisa	adult female	68	724±209	376±200	0.51±0.19	0.23±0.06	0.067±0.02	10:44:11	21	20.9	00:29:29
mocca	adult female	7	645±250	354±264	0.48±0.25	0.3±0.1	0.06±0.02	10:45:51	13	21.6	00:28:38
nora	adult female	2	661±28	227±125	0.34±0.17	0.21±0.02	0.061±0	10:54:00	22	22	00:28:26
piniata	adult female	1	631±NA	288±NA	0.46±NA	0.28±NA	0.06±NA	10:33:00	16	21	00:28:46
raffi	adult female	14	762±261	336±191	0.45±0.2	0.23±0.07	0.068±0.02	11:09:04	12	21.7	00:29:42
sarabi	adult female	16	725±173	273±104	0.39±0.13	0.26±0.05	0.064±0.02	11:20:41	17	22.3	00:29:48
sonya	adult female	2	1571±221	320±246	0.19±0.13	0.13±0.02	0.138±0.04	11:34:00	16	23	00:28:53
tiara	adult female	8	757±249	410±197	0.53±0.2	0.24±0.07	0.071±0.02	10:42:52	20	21	00:29:17
balu	flanged male	28	858±230	448±200	0.52±0.18	0.22±0.05	0.079±0.02	10:56:58	20	21.7	00:29:01
butterfly	flanged male	4	806±129	362±202	0.44±0.26	0.22±0.05	0.076±0.02	10:38:00	12	21.5	00:28:21
dian	flanged male	13	793±334	325±231	0.41±0.22	0.24±0.08	0.072±0.03	11:00:42	17	21.3	00:29:44
eddy	flanged male	3	863±200	551±230	0.62±0.16	0.17±0.03	0.084±0.02	10:20:20	19	18	00:34:01
fl	flanged male	1	502±NA	258±NA	0.51±NA	0.25±NA	0.07±NA	07:08:00	5	14	00:28:32
higer	flanged male	4	508±114	276±74	0.54±0.05	0.32±0.03	0.048±0.01	10:36:15	18	21	00:28:53
horseface	flanged male	3	898±190	647±96	0.73±0.1	0.18±0.03	0.086±0.02	10:30:00	15	21	00:28:38
islo	flanged male	28	967±323	592±288	0.6±0.2	0.19±0.05	0.087±0.03	11:07:13	18	22	00:29:06
kewin	flanged male	15	790±342	412±248	0.5±0.14	0.24±0.06	0.07±0.03	11:20:40	15	22.7	00:28:55
kombek	flanged male	6	416±81	254±77	0.6±0.13	0.27±0.03	0.042±0.01	09:54:00	20	19.3	00:29:30
kumango	flanged male	5	732±264	384±122	0.53±0.07	0.23±0.07	0.074±0.02	09:54:12	16	19.6	00:28:52
negi	flanged male	1	430±NA	118±NA	0.27±NA	0.37±NA	0.041±NA	10:26:00	16	20	00:29:49
otto	flanged male	11	965±375	575±258	0.58±0.18	0.21±0.06	0.089±0.03	10:47:44	13	21.4	00:29:05
pluto	flanged male	9	805±397	400±181	0.5±0.14	0.23±0.06	0.073±0.03	11:02:13	15	22.3	00:28:32
rakus	flanged male	2	906±84	485±286	0.55±0.37	0.16±0.01	0.083±0	10:57:30	12	22	00:28:36
saruman	flanged male	2	1454±1126	1254±1211	0.77±0.24	0.18±0.11	0.132±0.1	10:57:30	12	21.5	00:29:57
titan	flanged male	4	647±40	233±40	0.36±0.08	0.25±0.03	0.062±0.01	10:33:30	11	21	00:28:46
xenix	flanged male	7	1305±534	564±237	0.44±0.19	0.18±0.06	0.112±0.04	11:36:51	16	23	00:29:13
agam	independent immature	4	1152±366	186±93	0.19±0.16	0.2±0.05	0.098±0.03	11:40:30	14	23.2	00:28:52
chindy	independent immature	2	1110±143	796±114	0.72±0.01	0.15±0.02	0.115±0.01	09:38:00	14	19.5	00:28:56
cinnamon	independent immature	3	943±295	387±171	0.4±0.08	0.19±0.05	0.086±0.03	10:57:40	24	21.7	00:29:01
diddy	independent immature	6	801±147	249±75	0.32±0.1	0.26±0.07	0.07±0.01	11:25:00	22	22.3	00:29:22
ellie	independent immature	19	919±213	398±191	0.43±0.18	0.2±0.05	0.08±0.02	11:26:51	24	21.7	00:30:24
frankie	independent immature	3	1043±76	574±137	0.55±0.12	0.19±0.02	0.096±0.01	10:58:20	17	21.7	00:29:01
fredy	independent immature	7	1057±417	449±285	0.42±0.21	0.21±0.06	0.091±0.03	11:38:26	22	22.7	00:29:28
kronos	independent immature	1	1097±NA	360±NA	0.33±NA	0.19±NA	0.096±NA	11:24:00	23	23	00:28:30
lilly	independent immature	13	1054±276	543±195	0.52±0.14	0.18±0.05	0.093±0.02	11:15:09	23	22.1	00:29:23
lois	independent immature	24	661±195	362±162	0.53±0.15	0.25±0.07	0.067±0.02	09:46:05	18	19.4	00:28:46
nuzari	independent immature	1	789±NA	288±NA	0.37±NA	0.16±NA	0.07±NA	11:14:00	9	20	00:32:06
pauline	independent immature	1	697±NA	273±NA	0.39±NA	0.26±NA	0.061±NA	11:22:00	11	22	00:29:39
sazu	independent immature	1	658±NA	320±NA	0.49±NA	0.25±NA	0.068±NA	09:37:00	13	19	00:30:22
shera	independent immature	9	1033±272	363±169	0.37±0.17	0.19±0.03	0.091±0.02	11:23:33	24	22	00:29:55
tina	independent immature	12	743±225	355±169	0.47±0.15	0.22±0.04	0.066±0.02	11:12:25	22	21.9	00:29:32
trident	independent immature	6	1189±330	492±321	0.41±0.21	0.2±0.06	0.102±0.03	11:44:50	21	22.8	00:29:37
yulia	independent immature	10	939±223	317±158	0.34±0.15	0.23±0.04	0.083±0.02	11:14:06	18	22.3	00:28:56
aqra	unflanged male	5	799±211	291±211	0.34±0.2	0.22±0.03	0.077±0.02	10:15:00	12	20.4	00:29:53
balu	unflanged male	1	749±NA	455±NA	0.61±NA	0.2±NA	0.067±NA	11:15:00	16	22	00:29:21
bob	unflanged male	1	1050±NA	725±NA	0.69±NA	0.19±NA	0.101±NA	10:24:00	12	21	00:28:22
caesar	unflanged male	8	1030±424	453±181	0.44±0.09	0.2±0.06	0.092±0.04	11:13:38	22	22.5	00:28:40
derek	unflanged male	1	649±NA	59±NA	0.09±NA	0.33±NA	0.053±NA	12:11:00	26	24	00:29:14
dru	unflanged male	1	1124±NA	561±NA	0.5±NA	0.18±NA	0.1±NA	11:14:00	21	22	00:29:18
filip	unflanged male	3	982±330	613±307	0.6±0.11	0.22±0.08	0.092±0.04	10:53:00	20	22.3	00:27:59
gura	unflanged male	9	1205±521	508±252	0.44±0.15	0.18±0.05	0.104±0.05	11:31:53	21	22.9	00:29:06
horseface	unflanged male	5	805±383	453±286	0.53±0.14	0.25±0.12	0.074±0.04	10:55:36	20	21.8	00:29:01
jimmy	unflanged male	2	856±31	181±171	0.22±0.21	0.2±0.02	0.071±0	12:05:00	22	24	00:29:02
kiki	unflanged male	3	674±35	316±127	0.47±0.21	0.21±0.01	0.061±0	11:08:40	22	22.3	00:29:04
kopi	unflanged male	2	481±35	182±57	0.38±0.15	0.24±0.09	0.054±0	08:58:00	6	17	00:29:56
marco	unflanged male	1	593±NA	171±NA	0.29±NA	0.28±NA	0.048±NA	12:23:00	21	25	00:29:43
momok	unflanged male	1	1172±NA	683±NA	0.58±NA	0.2±NA	0.108±NA	10:53:00	13	22	00:28:23
nagini	unflanged male	3	619±168	349±72	0.57±0.08	0.27±0.03	0.057±0.01	10:42:40	16	21	00:29:13
rakus	unflanged male	6	978±307	359±289	0.34±0.19	0.2±0.05	0.088±0.03	11:20:10	24	22.3	00:29:10
saudade	unflanged male	1	732±NA	354±NA	0.48±NA	0.24±NA	0.062±NA	11:47:00	24	24	00:28:17
sem	unflanged male	1	878±NA	628±NA	0.72±NA	0.15±NA	0.084±NA	10:25:00	15	21	00:28:25
shane	unflanged male	1	1763±NA	916±NA	0.52±NA	0.14±NA	0.142±NA	12:24:00	14	24	00:31:00
smeagol	unflanged male	2	897±224	219±25	0.25±0.03	0.22±0.03	0.076±0.02	11:56:00	28	22	00:31:08
ulysses	unflanged male	3	890±429	190±38	0.25±0.1	0.22±0.09	0.079±0.04	11:38:00	21	23.3	00:28:41
unfl	unflanged male	1	1355±NA	1047±NA	0.77±NA	0.16±NA	0.137±NA	09:52:00	18	20	00:28:11
xenix	unflanged male	3	1186±188	466±254	0.38±0.18	0.16±0.02	0.099±0.01	11:54:40	16	21.3	00:32:15
zackey	unflanged male	1	1066±NA	584±NA	0.55±NA	0.2±NA	0.1±NA	10:42:00	14	22	00:27:55

C.3 Correlations between food availability and DJL and sinuosity index



(A) eFAI and DJL.

(B) hFAI and DJL.

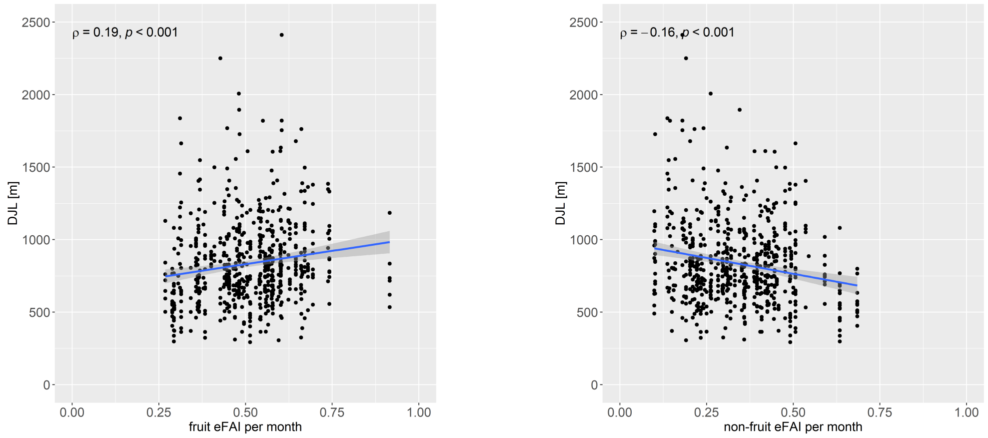
(C) eFAI and DJL per age-sex class.

(D) hFAI and DJL per age-sex class.

(E) eFAI and DJL for the two sexes.

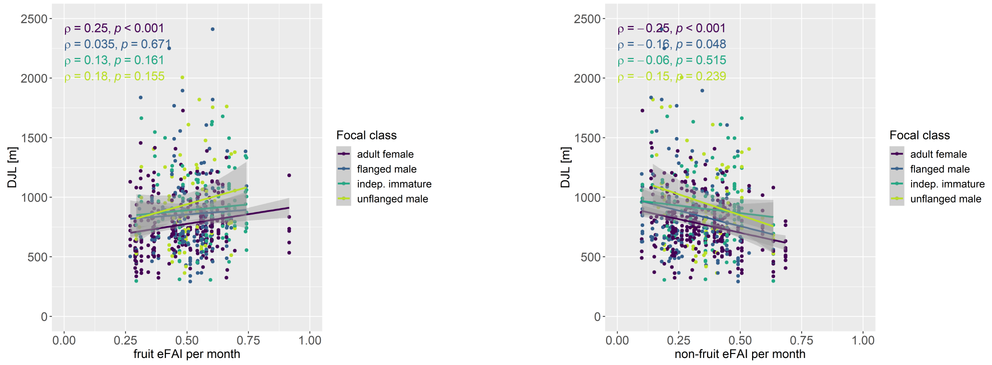
(F) hFAI and DJL for the two sexes.

FIGURE C.2: Correlations between the indices eFAI and hFAI and the day journey length for all data (A and B), per age-sex class (C and D) and divided for both sexes (E and F). Spearman's rho is indicating the degree of correlation and the p-value of the significance level.



(A) Fruit eFAI and DJL.

(B) Non-fruit eFAI and DJL.



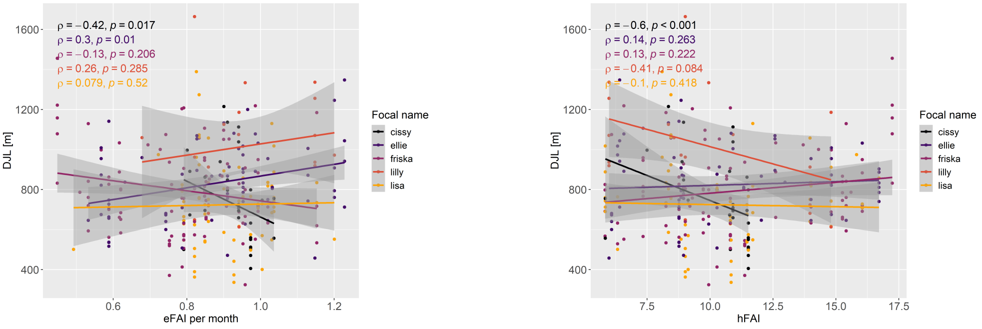
(C) Fruit eFAI and DJL per age-sex class.

(D) Non-fruit eFAI and DJL per age-sex class.

(E) Fruit eFAI and DJL for the two sexes.

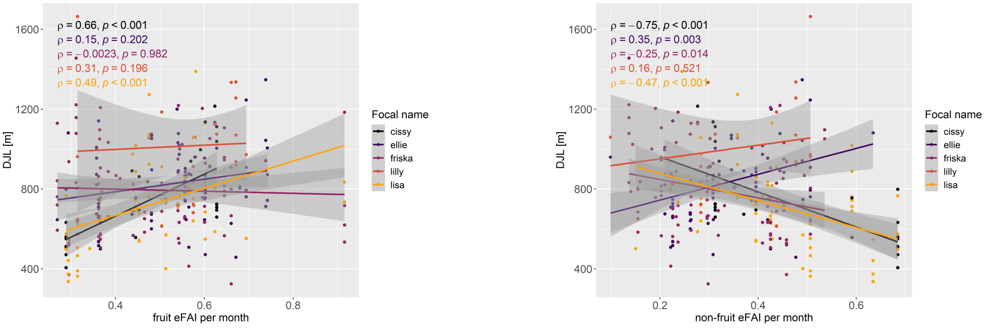
(F) Non-fruit eFAI and DJL for the two sexes.

FIGURE C.3: Correlations between the indices fruit eFAI and non-fruit eFAI and the day journey length for all data (A and B), per age-sex class (C and D) and divided for both sexes (E and F). Spearman's rho is indicating the degree of correlation and the p-value of the significance level.



(A) eFAI and DJL.

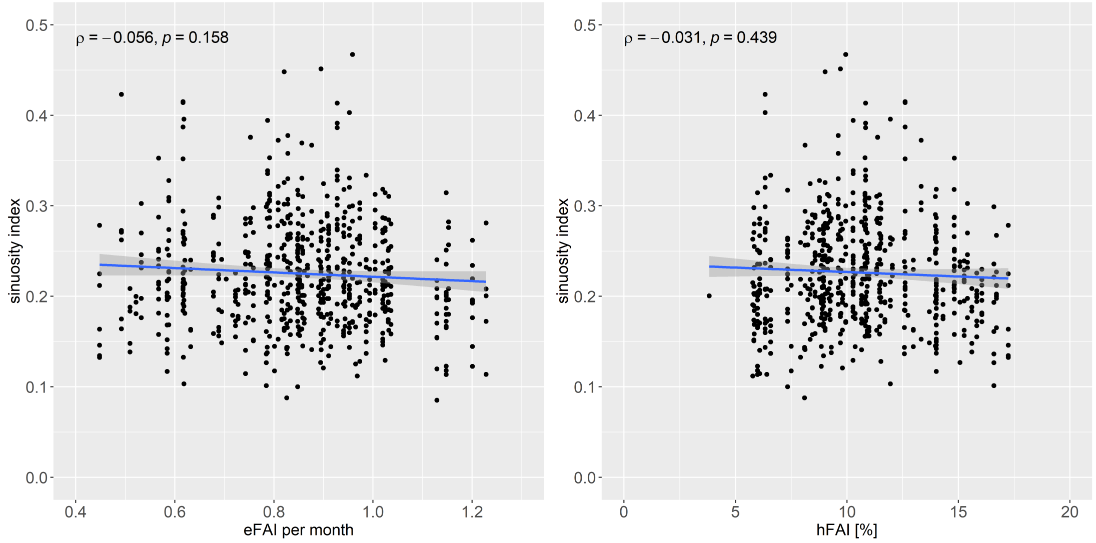
(B) hFAI and DJL.



(C) fruit eFAI and DJL.

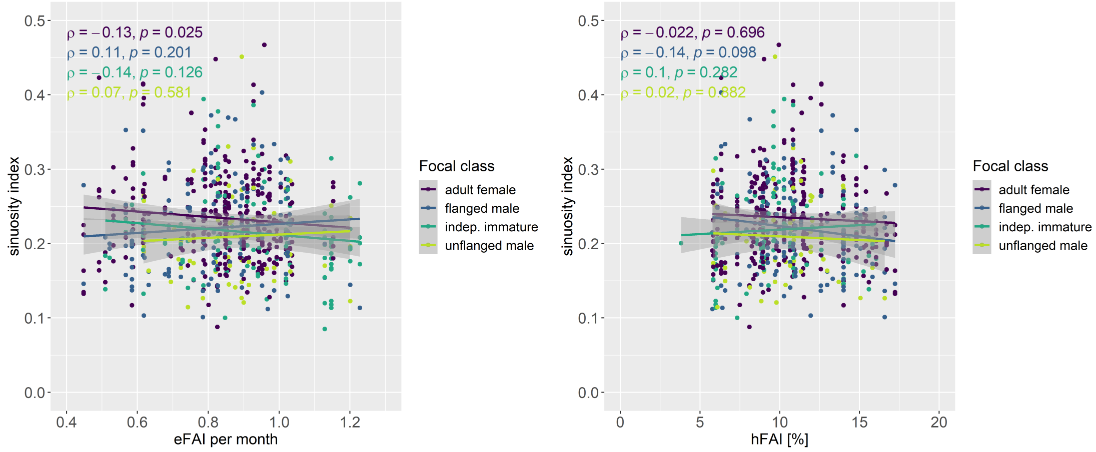
(D) non-fruit eFAI and DJL

FIGURE C.4: Correlations between the indices eFAI, hFAI, fruit eFAI, and non-fruit eFAI and DJL for five selected females. Spearman's rho is indicating the degree of correlation and the p-value of the significance level.



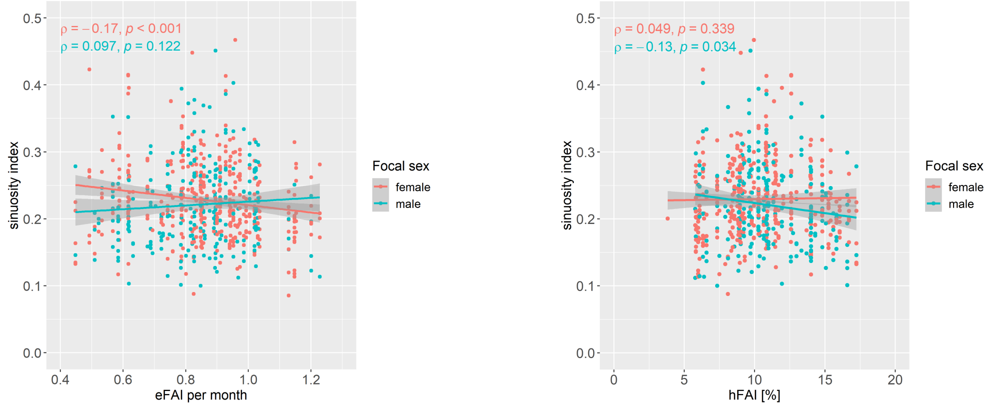
(A) eFAI and sinuosity.

(B) hFAI and sinuosity.



(C) eFAI and sinuosity per age-sex class.

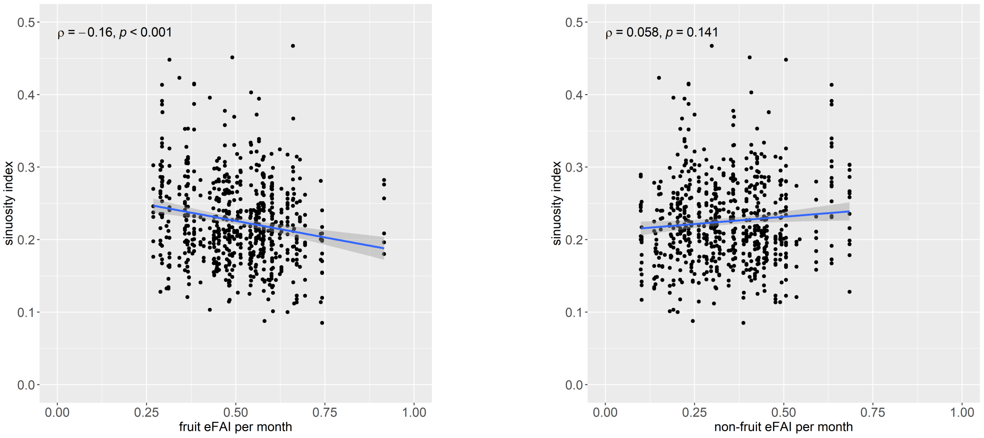
(D) hFAI and sinuosity per age-sex class.



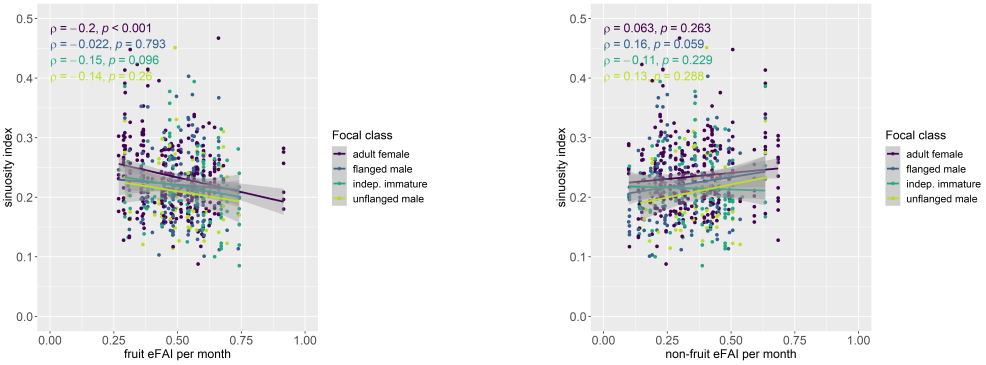
(E) eFAI and sinuosity for the two sexes.

(F) hFAI and sinuosity for the two sexes.

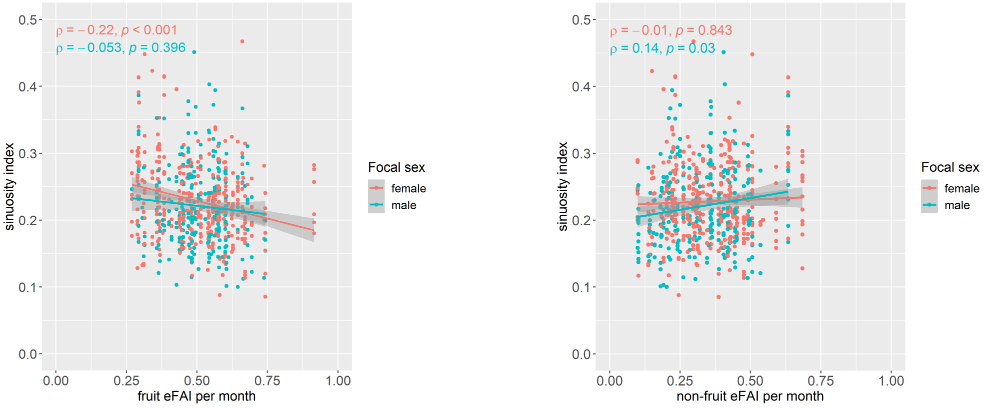
FIGURE C.5: Correlations between the indices eFAI and hFAI and the sinuosity index for all data (A and B), per age-sex class (C and D) and divided for both sexes (E and F). Spearman's rho is indicating the degree of correlation and the p-value of the significance level.



(A) Fruit eFAI and sinuosity. (B) Non-fruit eFAI and sinuosity.

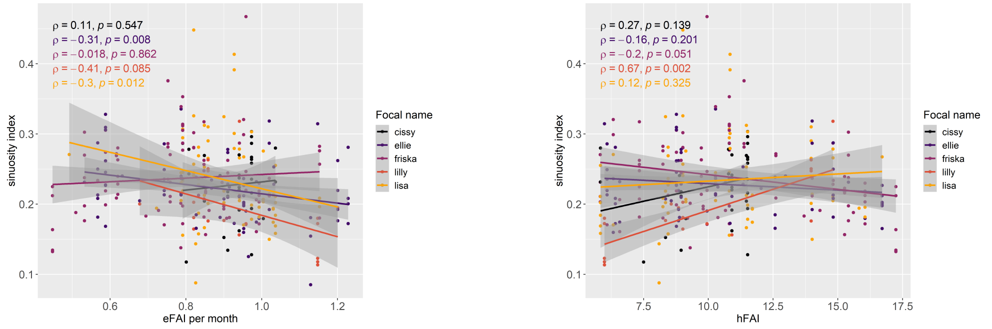


(C) Fruit eFAI and sinuosity per age-sex class. (D) Non-fruit eFAI and sinuosity per age-sex class.



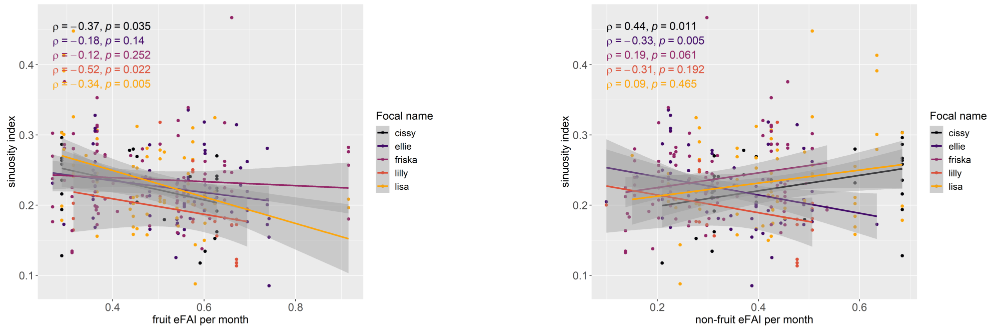
(E) Fruit eFAI and sinuosity for the two sexes. (F) Non-fruit eFAI and sinuosity for the two sexes.

FIGURE C.6: Correlations between the indices fruit eFAI and non-fruit eFAI and the sinuosity index for all data (A and B), per age-sex class (C and D) and divided for both sexes (E and F). Spearman's rho is indicating the degree of correlation and the p-value of the significance level.



(A) eFAI and sinuosity.

(B) hFAI and sinuosity.



(C) fruit eFAI and sinuosity.

(D) non-fruit eFAI and sinuosity

FIGURE C.7: Correlations between the indices eFAI, hFAI, fruit eFAI, and non-fruit eFAI and the sinuosity index for five selected females. Spearman's rho is indicating the degree of correlation and the p-value of the significance level.

C.4 Linear mixed-effects models for all 140 months

C.4.1 Day journey length

TABLE C.2: Statistical full models trying to explain the Day Journey Length (DJL) overall (a) and for males (b) and females (c) separately. Models include data from all the months without a minimum number of required follows per month.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	DJL of all age-sex classes (FO_DJL)	Intercept ***	Intercept	752.29	547.66 – 956.91	**<0.001**	-
	n = 735	hFAI	Fixed	7.46	-1.99 – 16.90	0.126	1.09
	p < 0.001 ***	fruit eFAI	Fixed	198.71	-24.72 – 422.14	0.085	1.07
	M-R^2 = 0.090	non-fruit eFAI ***	Fixed	-403.37	-625.54 – -181.21	**<0.001**	1.10
	C-R^2 = 0.381	Adult female - Flanged male	Fixed	25.74	-86.27 – 137.75	0.655	1.48
	Family = Gaussian	Adult female - Independent immature **	Fixed	126.61	33.32 – 219.90	**<0.01**	1.27
		Adult female - Unflanged male **	Fixed	173.77	55.24 – 292.29	**<0.01**	1.49
		Focal ***	Random	-	-	**<0.001**	-
		Month Year ***	Random	-	-	**<0.001**	-
b)	DJL of all males (FM_DJL)	Intercept ***	Intercept	940.14	567.59 – 1312.70	**<0.001**	-
	n = 303	hFAI	Fixed	5.43	-11.85 – 22.71	0.540	1.21
	p < 0.01 **	fruit eFAI	Fixed	181.32	-225.15 – 587.78	0.385	1.06
	M-R^2 = 0.066	non-fruit eFAI **	Fixed	-598.51	-991.63 – -205.39	**<0.01**	1.23
	C-R^2 = 0.342	Focal ***	Random	-	-	**<0.001**	-
	Family = Gaussian	Month Year *	Random	-	-	**0.025**	-
c)	DJL of all females (FF_DJL)	Intercept ***	Intercept	697.99	496.78 – 899.20	**<0.001**	-
	n = 432	hFAI	Fixed	6.51	-2.81 – 15.83	0.176	1.06
	p < 0.01 *	fruit eFAI *	Fixed	285.76	69.33 – 502.18	**0.012**	1.07
	M-R^2 = 0.034	non-fruit eFAI	Fixed	-192.07	-413.26 – 29.12	0.094	1.04
	C-R^2 = 0.476	Focal ***	Random	-	-	**<0.001**	-
	Family = Gaussian	Month Year ***	Random	-	-	**<0.001**	-

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

TABLE C.3: Statistical full models trying to explain the Day Journey Length (DJL) for all four age-sex classes separately. Models include data from all the months without a minimum number of required follows per month.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	DJL of flanged males only (FFM_DJL)	Intercept ***	Intercept	821.87	414.88 – 1228.87	**<0.001**	-
	n = 188	hFAI	Fixed	6.54	-12.12 – 25.19	0.496	1.23
	p = 0.039 *	fruit eFAI	Fixed	153.42	-312.31 – 619.14	0.522	1.04
	M-R^2 = 0.048	non-fruit eFAI *	Fixed	-476.18	-913.56 – -38.81	**0.039**	1.24
	C-R^2 = 0.249	Focal ***	Random	-	-	**<0.001**	-
	Family = Gaussian	Month Year	Random	-	-	0.492	-
b)	DJL of adult females only (FAF_DJL)	Intercept ***	Intercept	811.30	449.50 – 883.14	**<0.001**	-
	n = 354	hFAI	Fixed	9.60	-0.32 – 19.51	0.063	1.04
	p < 0.001 ***	fruit eFAI *	Fixed	271.43	36.46 – 506.41	**0.028**	1.09
	M-R^2 = 0.063	non-fruit eFAI *	Fixed	-306.56	-545.75 – -67.37	**0.015**	1.06
	C-R^2 = 0.507	Focal **	Random	-	-	**<0.01**	-
	Family = Gaussian	Month Year ***	Random	-	-	**<0.001**	-
c)	DJL of unflanged males only (FUM_DJL)	Intercept *	Intercept	1127.15	259.44 – 1994.87	**0.017**	-
	n = 66	hFAI	Fixed	-0.83	-41.92 – 40.27	0.969	1.18
	p = 0.05 *	fruit eFAI	Fixed	364.41	-534.95 – 1263.76	0.436	1.22
	M-R^2 = 0.133	non-fruit eFAI *	Fixed	-903.40	-1787.00 – -19.79	**0.051**	1.42
	C-R^2 = 0.447	Focal	Random	-	-	0.312	-
	Family = Gaussian	Month Year	Random	-	-	0.253	-
d)	DJL of independent immatures only (FII_DJL)	Intercept ***	Intercept	1080.86	584.25 – 1577.46	**<0.001**	-
	n = 127	hFAI	Fixed	5.34	-17.71 – 28.39	0.652	1.15
	p = 0.398	fruit eFAI	Fixed	-174.99	-746.80 – 396.82	0.552	1.04
	M-R^2 = 0.039	non-fruit eFAI	Fixed	-361.40	-908.61 – 185.80	0.203	1.10
	C-R^2 = 0.315	Focal	Random	-	-	0.196	-
	Family = Gaussian	Month Year *	Random	-	-	**0.026**	-

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

C.4.2 Total displacement distance

TABLE C.4: Statistical full models trying to explain Total Displacement Distance (TDD) overall (a) and for males (b) and females (c) separately. Models include data from all the months without a minimum number of required follows per month.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	TDD of all age-sex classes (FO_TDD)	Intercept ***	Intercept	456.59	290.43 – 622.76	**<0.001**	-
	n = 735	hFAI	Fixed	0.69	-7.04 – 8.41	0.862	1.09
	p = 0.111	fruit eFAI	Fixed	-22.48	-205.30 – 160.34	0.810	1.07
	M-R^2 = 0.037	non-fruit eFAI *	Fixed	-226.98	-408.56 – -45.40	**0.017**	1.10
	C-R^2 = 0.306	Adult female - Flanged male	Fixed	70.75	-15.49 – 156.98	0.116	1.46
	Family = Gaussian	Adult female - Independent immature	Fixed	17.68	-56.45 – 91.81	0.641	1.28
		Adult female - Unflanged male	Fixed	66.35	-26.44 – 159.14	0.166	1.46
		Focal ***	Random	-	-	**<0.001**	-
		Month Year ***	Random	-	-	**<0.001**	-
b)	TDD of all males (FM_TDD)	Intercept ***	Intercept	619.03	346.58 – 891.47	**<0.001**	-
	n = 303	hFAI	Fixed	-0.23	-12.80 – 12.35	0.972	1.21
	p = 0.013 *	fruit eFAI	Fixed	-77.61	-375.05 – 219.83	0.612	1.06
	M-R^2 = 0.047	non-fruit eFAI **	Fixed	-445.96	-730.01 – -161.92	**<0.01**	1.24
	C-R^2 = 0.244	Focal ***	Random	-	-	**<0.001**	-
	Family = Gaussian	Month Year	Random	-	-	0.327	-
c)	TDD of all females (FF_TDD)	Intercept ***	Intercept	357.33	196.16 – 518.50	**<0.001**	-
	n = 432	hFAI	Fixed	1.11	-6.65 – 8.88	0.779	1.06
	p = 0.950	fruit eFAI	Fixed	37.44	-143.50 – 218.37	0.687	1.07
	M-R^2 = 0.001	non-fruit eFAI	Fixed	-22.87	-207.52 – 161.79	0.809	1.04
	C-R^2 = 0.220	Focal ***	Random	-	-	**<0.001**	-
	Family = Gaussian	Month Year *	Random	-	-	**0.016**	-

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

TABLE C.5: Statistical full models trying to explain Total Displacement Distance (TDD) for all four age-sex classes separately. Models include data from all the months without a minimum number of required follows per month.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	TDD of flanged males only (FFM_TDD)	Intercept ***	Intercept	644.10	335.39 – 952.81	**<0.001**	-
	n = 188	hFAI	Fixed	-1.55	-15.58 – 12.49	0.829	1.33
	p = 0.092	fruit eFAI	Fixed	-124.66	-475.32 – 226.00	0.487	1.11
	M-R^2 = 0.035	non-fruit eFAI *	Fixed	-406.23	-732.94 – -79.53	**0.016**	1.22
	C-R^2 = 0.226	Focal ***	Random	-	-	**<0.001**	-
	Family = Gaussian	Month Year	Random	-	-	1	-
b)	TDD of adult females only (FAF_TDD)	Intercept ***	Intercept	325.99	147.63 – 504.35	**<0.001**	-
	n = 354	hFAI	Fixed	2.71	-5.92 – 11.35	0.541	1.04
	p = 0.761	fruit eFAI	Fixed	68.34	-139.40 – 276.07	0.523	1.09
	M-R^2 = 0.005	non-fruit eFAI	Fixed	-46.74	-254.78 – 161.29	0.661	1.06
	C-R^2 = 0.169	Focal	Random	-	-	0.197	-
	Family = Gaussian	Month Year **	Random	-	-	**<0.01**	-
c)	TDD of unflanged males only (FUM_TDD)	Intercept	Intercept	427.92	-175.94 – 1031.79	0.177	-
	n = 66	hFAI	Fixed	6.83	-22.68 – 36.33	0.653	1.16
	p = 0.181	fruit eFAI	Fixed	210.49	-415.69 – 836.67	0.518	1.19
	M-R^2 = 0.080	non-fruit eFAI	Fixed	-414.19	-1034.63 – 206.25	0.203	1.36
	C-R^2 = 0.311	Focal	Random	-	-	1	-
	Family = Gaussian	Month Year	Random	-	-	0.220	-
d)	TDD of independent immatures only (FII_TDD)	Intercept *	Intercept	533.85	120.52 – 947.18	**0.016**	-
	n = 127	hFAI	Fixed	0.10	-19.02 – 19.21	0.992	1.12
	p = 0.834	fruit eFAI	Fixed	-171.72	-657.76 – 314.31	0.494	1.03
	M-R^2 = 0.014	non-fruit eFAI	Fixed	-143.64	-604.69 – 317.40	0.546	1.09
	C-R^2 = 0.459	Focal *	Random	-	-	**0.024**	-
	Family = Gaussian	Month Year **	Random	-	-	**<0.01**	-

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

C.4.3 Sinuosity index

TABLE C.6: Statistical full models trying to explain sinuosity overall (a) and for males (b) and females (c) separately. Models include data from all the months without a minimum number of required follows per month.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	Sinuosity of all age-sex classes (FO_sinuosity)	Intercept ***	Intercept	0.2569	0.2135 – 0.3002	**<0.001**	-
	n = 735	hFAI	Fixed	-0.0009	-0.0030 – 0.0011	0.371	1.09
	p < 0.01 **	fruit eFAI *	Fixed	-0.0561	-0.1048 – -0.0073	**0.026**	1.07
	M-R^2 = 0.048	non-fruit eFAI	Fixed	0.0375	-0.0109 – 0.0858	0.132	1.10
	C-R^2 = 0.244	Adult female - Flanged male	Fixed	-0.0060	-0.0237 – 0.0118	0.514	1.38
	Family = Gaussian	Adult female - Independent immature	Fixed	-0.0132	-0.0299 – 0.0035	0.125	1.28
		Adult female - Unflanged male **	Fixed	-0.0288	-0.0493 – -0.0084	**<0.01**	1.35
		Focal **	Random	-	-	**<0.01**	-
		Month Year ***	Random	-	-	**<0.001**	-
b)	Sinuosity of all males (FM_sinuosity)	Intercept ***	Intercept	0.2051	0.1412 – 0.2689	**<0.001**	-
	n = 303	hFAI	Fixed	-0.0004	-0.0034 – 0.0026	0.790	1.21
	p = 0.098	fruit eFAI	Fixed	-0.0123	-0.0823 – 0.0577	0.731	1.06
	M-R^2 = 0.028	non-fruit eFAI *	Fixed	0.0721	0.0054 – 0.1388	**0.038**	1.23
	C-R^2 = 0.190	Focal **	Random	-	-	**<0.01**	-
	Family = Gaussian	Month Year	Random	-	-	0.156	-
c)	Sinuosity of all females (FF_sinuosity)	Intercept ***	Intercept	0.2818	0.2291 – 0.3345	**<0.001**	-
	n = 432	hFAI	Fixed	-0.0011	-0.0037 – 0.0014	0.382	1.07
	p = 0.013	fruit eFAI **	Fixed	-0.0968	-0.1566 – -0.0370	**<0.01**	1.06
	M-R^2 = 0.047	non-fruit eFAI	Fixed	0.0126	-0.0480 – 0.0731	0.686	1.05
	C-R^2 = 0.289	Focal *	Random	-	-	**0.025**	-
	Family = Gaussian	Month Year ***	Random	-	-	**<0.001**	-

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

TABLE C.7: Statistical full models trying to explain sinuosity for all four age-sex classes separately. Models include data from all the months without a minimum number of follows per month.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	Sinuosity of flanged males only (FFM_sinuosity)	Intercept ***	Intercept	0.1960	0.1258 – 0.2661	**<0.001**	-
	n = 188	hFAI	Fixed	0.0001	-0.0031 – 0.0033	0.957	1.25
	p = 0.173	fruit eFAI	Fixed	0.0074	-0.0731 – 0.0878	0.859	1.04
	M-R^2 = 0.030	non-fruit eFAI *	Fixed	0.0817	0.0070 – 0.1563	**0.040**	1.26
	C-R^2 = 0.168	Focal **	Random	-	-	**<0.01**	-
	Family = Gaussian	Month Year	Random	-	-	0.932	-
b)	Sinuosity of adult females only (FAF_sinuosity)	Intercept ***	Intercept	0.3102	0.2517 – 0.3686	**<0.001**	-
	n = 354	hFAI	Fixed	-0.0021	-0.0050 – 0.0007	0.146	1.04
	p < 0.01 **	fruit eFAI **	Fixed	-0.1165	-0.1856 – -0.0473	**<0.01**	1.08
	M-R^2 = 0.068	non-fruit eFAI	Fixed	0.0075	-0.0594 – 0.0745	0.826	1.06
	C-R^2 = 0.247	Focal	Random	-	-	1	-
	Family = Gaussian	Month Year **	Random	-	-	**<0.001**	-
c)	Sinuosity of unflanged males only (FUM_sinuosity)	Intercept **	Intercept	0.1830	0.0540 – 0.3120	**<0.01**	-
	n = 66	hFAI	Fixed	0.0013	-0.0051 – 0.0077	0.700	1.17
	p = 0.158	fruit eFAI	Fixed	-0.0598	-0.1891 – 0.0695	0.373	1.17
	M-R^2 = 0.076	non-fruit eFAI	Fixed	0.1060	-0.0253 – 0.2373	0.124	1.36
	C-R^2 = 0.115	Focal	Random	-	-	0.850	-
	Family = Gaussian	Month Year	Random	-	-	0.906	-
d)	Sinuosity of independent immatures only (FII_sinuosity)	Intercept ***	Intercept	0.2041	0.1138 – 0.2945	**<0.001**	-
	n = 127	hFAI	Fixed	-0.0001	-0.0043 – 0.0040	0.946	1.15
	p = 0.950	fruit eFAI	Fixed	0.0091	-0.0945 – 0.1126	0.864	1.05
	M-R^2 = 0.005	non-fruit eFAI	Fixed	0.0272	-0.0718 – 0.1261	0.593	1.10
	C-R^2 = 0.239	Focal	Random	-	-	0.165	-
	Family = Gaussian	Month Year *	Random	-	-	**0.033**	-

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

C.4.4 Straightness index

TABLE C.8: Statistical full models trying to explain the Straightness Index (SI) overall (a) and for males (b) and females (c) separately. Models include data from all the months without a minimum number of required follows per month.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	SI of all age-sex classes (FO_SI)	Intercept ***	Intercept	0.5471	0.4385 – 0.6556	**<0.001**	-
	n = 735	hFAI	Fixed	-0.0028	-0.0078 – 0.0022	0.280	1.09
	p = 0.016 *	fruit eFAI	Fixed	-0.0986	-0.2182 – 0.0211	0.110	1.10
	M-R^2 = 0.038	non-fruit eFAI	Fixed	0.0101	-0.1069 – 0.1272	0.866	1.11
	C-R^2 = 0.167	Adult female - Flanged male	Fixed	0.0551	-0.0041 – 0.1143	0.076	1.40
	Family = Gaussian	Adult female - Independent immature	Fixed	-0.0443	-0.0984 – 0.0098	0.111	1.29
		Adult female - Unflanged male	Fixed	-0.0224	-0.0887 – 0.0439	0.510	1.36
		Focal ***	Random	-	-	**<0.001**	-
		Month Year	Random	-	-	0.241	-
b)	SI of all males (FM_SI)	Intercept ***	Intercept	0.6425	0.4679 – 0.8171	**<0.001**	-
	n = 303	hFAI	Fixed	-0.0032	-0.0112 – 0.0047	0.425	1.22
	p = 0.195	fruit eFAI	Fixed	-0.1445	-0.3339 – 0.0449	0.136	1.07
	M-R^2 = 0.016	non-fruit eFAI	Fixed	-0.1750	-0.3523 – 0.0023	0.054	1.26
	C-R^2 = 0.216	Focal ***	Random	-	-	**<0.001**	-
	Family = Gaussian	Month Year	Random	-	-	1	-
c)	SI of all females (FF_SI)	Intercept ***	Intercept	0.5107	0.3878 – 0.6336	**<0.001**	-
	n = 432	hFAI	Fixed	-0.0031	-0.0091 – 0.0029	0.311	1.05
	p = 0.119	fruit eFAI	Fixed	-0.1067	-0.2458 – 0.0323	0.140	1.08
	M-R^2 = 0.015	non-fruit eFAI	Fixed	0.0972	-0.0447 – 0.2390	0.186	1.04
	C-R^2 = 0.080	Focal *	Random	-	-	**0.049**	-
	Family = Gaussian	Month Year	Random	-	-	0.687	-

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

TABLE C.9: Statistical full models trying to explain the Straightness Index (SI) for all four age-sex classes separately. Models include data from all the months without a minimum number of required follows per month.

Nr.	Response variable / Model description	Factor	Factor type	Estimate	Confidence Interval	P	VIF
a)	SI of flanged males only (FFM_SI)	Intercept ***	Intercept	0.6754	0.4472 – 0.9036	**<0.001**	-
	n = 188	hFAI	Fixed	-0.0029	-0.0134 – 0.0077	0.598	1.21
	p = 0.532	fruit eFAI	Fixed	-0.1659	-0.4292 – 0.0975	0.221	1.04
	M-R^2 = 0.014	non-fruit eFAI	Fixed	-0.1258	-0.3731 – 0.1215	0.323	1.22
	C-R^2 = 0.207	Focal **	Random	-	-	**<0.01**	-
	Family = Gaussian	Month Year	Random	-	-	0.157	-
b)	SI of adult females only (FAF_SI)	Intercept ***	Intercept	0.4955	0.3612 – 0.6297	**<0.001**	-
	n = 354	hFAI	Fixed	-0.0042	-0.0108 – 0.0024	0.218	1.03
	p = 0.127	fruit eFAI	Fixed	-0.0563	-0.2136 – 0.1009	0.487	1.11
	M-R^2 = 0.019	non-fruit eFAI	Fixed	0.1420	-0.0152 – 0.2992	0.084	1.08
	C-R^2 = 0.056	Focal	Random	-	-	0.235	-
	Family = Gaussian	Month Year	Random	-	-	0.746	-
c)	SI of unflanged males only (FUM_SI)	Intercept	Intercept	0.4561	-0.0199 – 0.9320	0.070	-
	n = 66	hFAI	Fixed	0.0003	-0.0227 – 0.0233	0.978	1.16
	p = 0.995	fruit eFAI	Fixed	0.0262	-0.4761 – 0.5285	0.919	1.21
	M-R^2 = 0.001	non-fruit eFAI	Fixed	-0.0356	-0.5258 – 0.4546	0.888	1.38
	C-R^2 = 0.446	Focal	Random	-	-	1	-
	Family = Gaussian	Month Year *	Random	-	-	0.015	-
d)	SI of independent immatures only (FII_SI)	Intercept **	Intercept	0.4002	0.1329 – 0.6675	**<0.01**	-
	n = 127	hFAI	Fixed	0.0011	-0.0114 – 0.0135	0.869	1.11
	p = 0.991	fruit eFAI	Fixed	0.0385	-0.2700 – 0.3470	0.809	1.04
	M-R^2 = 0.0007	non-fruit eFAI	Fixed	-0.0048	-0.2969 – 0.2872	0.974	1.07
	C-R^2 = 0.328	Focal **	Random	-	-	**<0.01**	-
	Family = Gaussian	Month Year	Random	-	-	0.412	-

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

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.

T. Riegger ……………………………… Zürich, 31.8.2022 ………………………………

Tobias Riegger Place / Date