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DIET, COGNITION, AND NUTRIENT BALANCING IN AN ORANGUTAN HABITAT

By

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ABSTRACT OF THE DISSERTATION

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In complex environments, the ability to encode information about the location of resources should confer selective advantages by improving foraging efficiency. What constitutes foraging goals, and to what degree species encode information about food resources remain largely unresolved. In this dissertation, I apply principles from nutritional geometry and movement ecology to 1) examine whether macronutrient balancing is a biologically relevant foraging goal for Bornean orangutans; and 2) investigate the relationship between preference indices and the nutritional geometry of orangutan foods, and 3) explore the ways in which movement and spatial cognition facilitate nutritional balancing. Orangutans were chosen as a model system because of their capacity for complex cognition, their solitary social system, and the high variability in food availability in orangutan habitats.

In Chapter 2, simulation and Behavioral Change Point Analysis are used to demonstrate that the balance of nutrient intake by orangutans cannot be attributed to chance, and that individuals modulate their movement behavior in response to nutrient intake in a goal directed manner. In Chapter 3, nutritional isocline plots and food electivity indices are used to demonstrate that the orangutans' evaluation of food quality is significantly related to nutritional balancing. Items of high nutritional return are preferred and associated with fast trajectories

through nutritional cartesian space. In Chapter 4, a continuous-space continuous-time movement framework (ctmm) is utilized to characterize patterns of space use by Bornean orangutans, and remote sensing and simulation modeling are used to evaluate different cognitive movement strategies in the context of nutritional balancing. Multispectral analysis and supervised machine learning techniques are used to map the nutritional landscape at Tuanan. Movement parameters from the ctmm analysis are used to parameterize models simulating memory and perception-based strategies of nutrient balancing. Simulation results suggest orangutans utilize spatial memory to facilitate nutritional balancing.

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Table of Contents

Abstract	ii
Acknowledgements	iv
Table of Contents	vii
List of Figures	x
List of Tables	xii
List of Equations	xiii
Chapter 1: Introduction	1
1.1 Synopsis	1
1.2 Organization of this Dissertation	2
1.3 Introduction	3
1.3.2 Cognitive Maps	5
1.3.3 Encoding information	8
1.3.4 Selection and cognitive maps.....	10
1.3.5 Predicting space use and foraging success.....	12
1.3.6 Empirical studies on spatial memory in wild animals.....	19
1.3.7 Study System	24
1.3.8 Study site and population.....	25
References	32
Chapter 2. Variation in spatial movement as it relates to nutritional balancing in Bornean orangutans (<i>Pongo pygmaeus wurmbii</i>)	38
2.1. Introduction	38
2.2. Methods	43
2.2.1 Study site and system.....	43
2.2.2 Behavioral data collection.....	43
2.2.3 Nutrient intake	45
2.2.4 Simulation	47
2.2.5 Goal directed behavior	48
2.3. Results	51
<i>Hypothesis 2.1</i>	51
<i>Hypothesis 2.2</i>	57
2.4. Discussion and Conclusion	59
References	65

Chapter 3. Food electivity and macronutrient balancing by Bornean orangutans (<i>Pongo pygmaeus wurmbii</i>)	68
3.1. Introduction	68
3.2. Methods	73
3.2.1 Study site and system	73
3.2.2 Behavioral data collection	73
3.2.3 Nutrient intake and balancing	74
3.2.4 Nutritional intake rate and isoclines	75
3.2.5 Vanderploeg and Scavia's E^*	75
3.2.6 Statistical analyses	76
3.3. Results	76
3.4. Discussion and Conclusion	83
References	86
Chapter 4. Orangutan space use and strategies for balancing nutrients.	88
4.1 Introduction	88
4.2 Methods	94
4.2.1 Study site and system	94
4.2.2 Behavioral data collection	94
4.2.3 Phenology	94
4.2.4 Nutrient intake	95
4.2.5 Software	95
4.2.6 Nutritional mapping	96
4.2.7 Movement analysis	99
4.2.8 Simulation	103
4.3 Results	109
4.3.1 Movement analysis	109
4.3.2 Tree classification and nutrient mapping	119
4.3.3 Simulation results	124
4.4 Discussion and Conclusion	126
4.4.1 <i>Home range utilization</i>	126
4.4.2 <i>Male-female differences in space use</i>	126
4.4.3 <i>Home range overlap</i>	128
4.4.4 <i>Travel distance between food patches</i>	130

4.4.5 <i>Nutritional mapping</i>	131
4.4.6 <i>Simulation</i>	131
References	134
Chapter 5. Conclusion	142
5.1 Summary and conclusions	142
5.2 Future work	144
5.3 Conclusion	145
References	147

List of Figures

Figure 1.1	26
Figure 1.2	27
Figure 1.3	28
Figure 1.4	29
Figure 2.1	52
Figure 2.2	54
Figure 2.3	55
Figure 2.4	57
Figure 2.5	58
Figure 2.6	58
Figure 3.1	77
Figure 3.2	78
Figure 3.3	78
Figure 3.4	79
Figure 3.5	81
Figure 3.6	82
Figure 3.7	83
Figure 4.1	101
Figure 4.2	107
Figure 4.3	110
Figure 4.4	112
Figure 4.5	113
Figure 4.6	114
Figure 4.7	116
Figure 4.8	118

Figure 4.9	119
Figure 4.10	120
Figure 4.11	123
Figure 4.12	125

List of Tables

Table 1.1	30
Table 2.1	45
Table 2.2	47
Table 2.3	50
Table 2.4	53
Table 2.5	59
Table 3.1	79
Table 4.1	108
Table 4.2	111
Table 4.3	113
Table 4.4	115
Table 4.5	116
Table 4.6	120

List of Equations

Equation 2.1a	45
Equation 2.1b	45
Equation 2.2a	47
Equation 2.2b	47
Equation 2.3	47
Equation 2.3a	47
Equation 2.4a	47
Equation 2.4b	48
Equation 2.5	48
Equation 2.6	49
Equation 2.7a	49
Equation 2.7b	49
Equation 4.1a	104
Equation 4.1b	104
Equation 4.2	104
Equation 4.3	106
Equation 4.4	108
Equation 4.5a	108
Equation 4.5b	108

Chapter 1: Introduction

1.1 Synopsis

Field research on the diet and behavior of animal systems is now reaching a new state of maturation, where long-term datasets on a number of taxa are becoming available. The accumulation of continuous longitudinal data on ecosystem structure, dynamics, and diversity, as well as lifetime records of the behavior and reproduction of individual animals, are starting to converge. This has created opportunities to ask new, large scale ecological questions, in addition to addressing previously intractable questions on a number of difficult to study systems. As a result, there has been a recent and rapid swell in the development of interdisciplinary techniques to quantitatively address these data.

In the realm of feeding ecology, technological advancements in animal tracking (Wilkel et al., 2007; Brown et al., 2012; Kays et al., 2015) and remote sensing technologies (Lim et al., 2003; Asner et al., 2008; Adam et al., 2010), new urinalysis assays (Emery Thompson et al., 2008; Vogel et al., 2012), and many novel analytical frameworks are all available in this era of long term data. Prior to this current era of research, studies have struggled to address how animals navigate the **what**, **when**, and **where** of decision making in the wild. Studying what animals know about their resources and how they utilize that knowledge requires somewhat complete knowledge about that animal's environment (Janson and Byrne, 2007).

In this dissertation, I present data from a field study on Bornean orangutans (*Pongo pygmaeus wurmbii*) at the Tuanan Orangutan Research Station from 2014-2015. These data were collected as part of the Tuanan Orangutan Research Project; a large scale collaboration between Rutgers University, University of Zurich, and Universitas Nasional Jakarta. The goals of this study are to understand the underlying processes that generate both fine scale and large scale

patterns in the spatial movement of individuals; to reevaluate our understanding of foraging goals and what constitutes them; and study the relationships between macronutrients and ecosystem structure as they pertain to plant-animal interactions; and to take advantage of the new methods and technologies to develop a framework for studying memory as a mechanism for goal directed behavior.

1.2 Organization of this Dissertation

In this chapter, I introduce the background theory and literature for this study. I describe the study system, and present the metadata about the individual orangutans analyzed here. Each of the following chapters are written as a manuscript for publication, and have separate methods sections. There is significant overlap in the methods used to answer the questions addressed in each chapter. In chapter two, I construct simulations to evaluate whether nutritional balancing in this study system is an environmental artifact, or a biologically meaningful signal. I then use behavioral segmentation techniques to evaluate whether individuals are treating this metric as a foraging goal, and discuss the relevance of expanding our understanding of goals beyond net calories. In chapter three, I analyze various physical and chemical attributes of trees and food items and how they may drive dietary electivity indices. I then discuss how these relationships can be integrated into the Geometric Framework of Nutrition to quantify the value of a particular goal resource. In chapter four, I utilize the emerging continuous space continuous time modeling framework to analyze large scale ranging and home-range behavior to revisit our understanding of orangutan home-range use. I then develop spatially explicit maps of the nutritional landscape from remotely sensed data to examine the drivers of fine scale spatial decisions, and model whether memory may be a mechanism allowing individuals to acquire food. Finally, in chapter 5 I conclude by giving a brief synopsis of the results in each chapter.

1.3 Introduction

There is a long and rich history of research on the diets and foraging behavior of animals. Starting with seminal papers by Emlen (1966), MacArthur and Pianka (1966), and Schoener (1971), scientists have tried to understand how natural selection has shaped the diets and foraging behavior of animal systems, assuming that foraging strategies are a function of fitness maximization. Because animals are invariably required to feed in order to survive and reproduce, foraging decisions are thought to be based on a set of economic rules that allow individuals to maximize efficiency, whereby the relevant currency is usually assumed to be energy (Schoener 1971; Krebs 1974). These decision-making rules are the basis for the optimal foraging literature, and much effort has gone into studying if and how individuals forage in an “optimal” way.

A major tenant of optimal foraging theory is that animals are trying to maximize foraging efficiency given a set of constraints (Schoener 1971; Krebs 1974). The most fundamental extrinsic constraints on foraging are the spatiotemporal availability of food, and time, whereby time is a limited resource and individuals attempt to maximize energy intake or minimize the amount of time spent searching for and processing food (Krebs 1974; Pyke et al. 1977). Research on how this optimization is achieved has therefore been split between four broad categories (Pyke et al. 1977): 1) What items to include in the optimal diet? 2) How to choose between food patches? 3) How much time to commit to each patch? 4) How to optimize movement between patches? For a long time, the latter of these four received the least amount of attention; however, due to advances in modeling, the increased number of long-term datasets, and technological advances enabling empirical studies on of the subject, there has been a recent shift in attention towards animal space use in the context of foraging. This discussion will focus on the questions and key issues associated with animal movement and foraging theory.

Two seminal studies helped set the stage for the current work on spatial movement and foraging, and serve as a foundation for the present discussion (Cody, 1971; Pyke, 1974)). Animal movement is generally present in the form a track representing the animal's travel path. An animal's movement track is the continuous stochastic process resulting from the interaction of behavior with physiological and environmental constraints; however, the data that are actually obtained by sampling an animal's movement are discretely sampled subsets of that continuous movement process. Data representing movement tracks therefore typically consist of some distribution of steps or step-lengths (the distance between the discretely sampled locations) and turns (changes in angles between discretely sampled locations) (Nathan 2008, Gurarie 2009, Schick et al. 2008, Fleming 2014). Since the 1930's, entomologists have reported changes in turning angles of animals upon encountering a food item, but very few studies addressed broader evolutionary questions about how such changes are influenced by distribution and foraging context (Pyke et al. 1977). These questions were first formally addressed by evolutionary biologists Cody (1971) and Pyke (1974) by comparing simulated data with available empirical data on mixed flock fringillid birds (families Cardinalidae, Emberizidae, Fringillidae, Parulidae, Picidae, Regulidae, Troglodytidae, Tyrannidae, and Vireonidae) and hummingbirds (*Selasphorus platycercus*) respectively. Both authors argued that foraging efficiency would be maximized if animals avoid revisiting previously exploited food patches, assuming that patches are depleted upon visitation (Cody 1971; Pyke 1974; Pyke et al. 1977). They also assumed that animals are foraging with only local information (stimuli from the current position), and therefore movement decisions are not influenced by outside or non-local information (i.e., stimuli from or knowledge about far away resources) (Cody 1971; Pyke, 1974). The results of their studies showed that patch revisitation was indeed minimized when movement was linear, changes in direction were

restricted to the boundary of the foraging environment, and that these model outputs were consistent with the available empirical data (Cody 1971; Pyke 1974). Pyke later reviewed the available literature to test whether these results were consistent across animals, but found that animal movement varied widely across taxa and were rarely consistent with their original simulations (Pyke 1978a, Pyke et al. 1977). In a following study, Pyke (1978b) found that changes in travel paths of bumblebees were influenced by non-local information. Pyke found that bumblebees navigate between flowers by conducting local scans from the current flower to locate and travel to the nearest detectable flower (Pyke 1977). Pyke (1977) suggests that failure to replicate Cody (1971) and Pyke's (1974) original findings across a wide variety of taxa is most likely because the assumption that travel decisions are based only on local information is incorrect; and that there are cases whereby animals are likely using outside information to make travel decisions.

If animals are using both local and non-local spatial information to maximize foraging efficiency, then natural selection must have resulted in adaptations that minimize errors and facilitate the storage of information (Bennett 1996). The current literature seems to be converging on spatial memory and the associated cognitive adaptations as the mechanisms by which optimal travel decisions are made while foraging (e.g. Janson 2000; Janson and Byrne 2007; Gautestad 2011; Fagan et al. 2013).

1.3.2 Cognitive Maps

Spatial memory is often presented as an abstraction whereby animals “map” spatial information, potentially onto some sort of mental image commonly referred to as a cognitive map (e.g., Gallistel 1989; Bennett 1996). Although there are a wide variety of published definitions of cognitive maps (see Bennett 1996 for a list of definitions), the majority of them

have limited utility because they are too vague or do not allow explicit predictions to be made about behavior (Bennett 1996). The original concept of a cognitive map, and the coining of the term, was by Tolman (1948), who defined cognitive maps as mental representations of routes, paths, and environmental relationships that determine an animal's behavioral response. He explained that the diagnostic feature of a cognitive map is that it allows animals to make novel shortcuts between two locations independently of current environmental stimuli (Tolman 1948). Tolman's (1948) concept of the cognitive map was expanded upon by O'Keefe and Nadel (1978) who distinguished between maps and routes, where routes were presented as a simpler alternative to cognitive maps. Route-based navigation simply involves the use of straight movement between landmarks to achieve foraging goals (O'Keefe and Nadel 1978). Routes require the storage of very little information and can therefore result advantageously in faster travel due to the relatively simpler calculations required, but routes are also very rigid and extremely sensitive to damage or loss of landmarks (O'Keefe and Nadel 1978). Cognitive maps differ from this system in that they 1) are extremely flexible and insensitive to the loss of landmarks; 2) contain vast amounts of spatial information; and 3) result in more direct but slower travel since they demand more complex calculations (O'Keefe and Nadel 1978).

The value of this original concept of a cognitive map is that it provides a clear set of predictions about the behavior of individuals under identified conditions (Bennett 1996). Tolman (1948) originally provided evidence from captive experiments on rats (*Rattus norvegicus*) and argued that their ability to make novel shortcuts suggests that they have cognitive maps. O'Keefe and Nadel (1978) lent further support to this conclusion in their brief review of data on wolves (*Canis lupus*) and their ability to make novel short cuts. Bennett (1996) however, cautioned against defining cognitive maps in this manner. He indirectly invoked Morgan's Canon

(1903), and explained that demonstration of a novel behavioral short cut requires data that reject simpler mechanisms that could have led to the same navigational outcome (Bennett 1996).

Bennett (1996) identifies three such alternative scenarios that must be eliminated before one can confidently claim that a novel short cut was made, and therefore, that there is a cognitive map (*sensu* Tolman 1948). The first possibility is that the short cut is, in fact, not truly novel, and that the animal has performed the “short cut” based on prior experience unbeknownst to the observer. The second, and most obvious alternative, is that the animal did not perform route based travel as per O’Keefe and Nadel (1978), i.e., the animal follows a seemingly novel path from one location to another simply because it recognizes a landmark from a new angle (and not because it possesses any detailed representations about the location of its goal). Finally, it must be shown that the short cut is not a product of path integration. Path integration, also known as “dead reckoning”, is a method of navigation whereby an animal returns to its starting point by summing the vectors of distance and direction to estimate its current position, and then calculating a direct return to the starting point (Gallistel 1989; Bennett 1996; Etienne and Jeffery 2004). This form of navigation requires minimal memory, but is not a cognitive map, and is common in arthropods and vertebrates (Gallistel 1989; Bennett 1996; Etienne and Jeffery 2004). Bennett (1996) asserts that there are no cases where all simpler solutions can be confidently ruled out, and therefore Tolman’s (1948) concept of cognitive maps should not be invoked as an explanation.

Another definition of a cognitive map is simply a record in an animal’s brain of geometric relationships between locations in space (Gallistel 1989; Gallistel 1993; Gallistel 1994). In this case, types of cognitive maps differ only in the types of geometries that are encoded by the animal and govern its decisions (Gallistel 1989). Under this definition, there is no

distinction between route based travel systems or map based travel systems, both are considered forms of cognitive maps (Bennett 1996). This conceptualization of cognitive maps has advantages over the original Tolman (1948) concept in that it implies all animals have a mental geometric representation of space. Since different types of cognitive map differ in the types of geometries that are encoded, researchers studying spatial memory are able to formally test predictions derived from those geometries, and behavior can be explicitly tested against formal mathematical models of animal space use (O'Keefe and Bennett 1994).

1.3.3 Encoding information

Regardless of what definition of cognitive map one chooses to accept, what is consistent across each conceptual variant is that spatial information is somehow “mapped” onto the brain itself. This leaves us with the question of how spatial information is actually biologically encoded, and which features selection is acting on to enable animals to use cognitive maps? O'Keefe and Nadel (1978) were the first to propose that cognitive maps are encoded by the hippocampus. There was, however, debate about hippocampal function and how memory is encoded. Stemming from independent bodies of work; namely evidence linking hippocampal damage to amnesia, and work demonstrating neuronal activity in the hippocampus during navigation, there was disagreement about whether the hippocampus was responsible for encoding declarative memory, which is consciously recalled memory such as facts or verbal information (see Ullman (2004)), or encoding spatial memory (Scoville & Milner 1957; O'Keefe & Dostrovsky, 1971; Schiller et al. 2015)). Because these lines of research differed substantially in their methods, it was difficult to come to a consensus about the role of the hippocampus (Schiller et al. 2015).

Recently, a substantial amount of work has emerged allowing for both views of hippocampal function to converge (Buzsáki & Moser 2013; Milivojevic & Doeller 2013; Maguire & Mullally 2013; Eichenbaum & Cohen 2014; Schiller et al. 2015). A recent and detailed synthesis by Schiller et al. (2015) discussed how neuronal activity in the hippocampus is associated with multiple types of spatial and non-spatial information. Citing evidence from fMRI and neuronal recordings, they discuss how both spatial and temporal information is encoded by the hippocampus. They report reliable firing sequences of hippocampal neurons in both temporal and spatial contexts, and that the temporal coding of hippocampal neurons parallels spatial coding of hippocampal neurons (Schiller et al. 2015). They also discuss several recent studies demonstrating that associated spatial and non-spatial variables are encoded together, and that spatial and non-spatial context are integrated and organized into networks of multiple related memories (Schiller et al. 2015). What's even more interesting is their suggestion that grid cells in the medial entorhinal cortex make computations regardless of the types of sensory inputs a species relies on (Schiller et al. 2015). They suggest that despite reliance on disparate sensory modalities (e.g., vision for primates and smell for rats), rats and primates may use the same neuronal coding mechanisms (Schiller et al. 2015), implying that computations by grid cells are not bound to sensory mechanism, movement, or body orientation and reflect navigation through mental space (Schiller et al. 2015). This suggestion that similar processes are at work regardless of the means of sensory perception should be taken into account when controlling for the perceptual range of an individual in studies of spatial foraging.

Tolman (1948) described novel short cuts as the primary feature of cognitive maps, however he described their primary function as support for the planning of behavior to obtain goals (Tolman 1948). Schiller et al. (2015) demonstrate that cognitive maps are

multidimensional and experiences are mapped across many behavioral domains. What is clear from Schiller et al.'s (2015) discussion of the hippocampus is that cognitive maps are not only records of geometric relationships in space, but also temporal relationships and potentially other types of attribute information associated with particular mapped goals. Schiller et al.'s (2015) expanded concept of a multidimensional cognitive map allows us to expand our predictions about how an optimal forager will make travel decisions beyond just geometries.

1.3.4 Selection and cognitive maps

Cognitive maps should provide many potential selective advantages to individuals that possess them. At large scales, cognitive maps should aid in navigating spatially complex landscapes, locating and relocating rare or essential sites more efficiently, or obtaining resources that are temporally variable (Bingman & Cheng 2005; Janmaat et al. 2006; Janson & Byrne 2007; Papastamatiou et al. 2013, Fagan et al. 2013). At local scales, cognitive maps may result in better access to critical resources or locations (Janson 2000, Fagan et al. 2013). Perhaps the best empirical evidence for selection on cognitive maps is the body of work on food-caching chickadees (genus *Poecile*). Food-caching behavior is characterized by non-migratory animals collecting and storing food during times of food abundance, and relying heavily on these stored foods during times of food scarcity or high variability (Vander Wall 1990; Pravosudov and Roth 2013). Croston et al. (2015) stated that variation in intensity of the food scarcity period is predictable along climatic gradients, and therefore predict that chickadee reliance on food-caches should vary with respect to the intensity of those periods. Furthermore, because food-caching behavior is dependent on the cognitive processes involved in spatial memory, (Krebs et al. 1989; Sherry et al. 1989; Dukas 2004; Pravosudov and Roth 2013) Croston et al. (2015) predicted that spatial memory and the associated anatomy should vary with respect to reliance on food-caching.

They embarked on a lengthy review and synthesis on the literature on food-caching chickadees in order to discuss four potential contributors to variation in food-caching, the hippocampus, and spatial memory. These contributors are local adaptation, behavioral plasticity, development, and epigenetics (Croston et al. 2015). A very important aspect of their review as it pertains to the present discussion are that in a series of studies, birds collected from different climates and populations, yet reared under the same conditions, showed significant differences in spatial memory, number of hippocampal neurons, rates of hippocampal neurogenesis, and hippocampal morphology (reviewed in Croston et al. 2015). Additionally, during interspecific social interactions between chickadee species, chickadee populations from harsher climates were consistently dominant over those from other populations, restricting access to critical resources to individuals from local populations (Croston et al. 2015). Furthermore, they reported strong female preference for males from their own population (Croston et al. 2015). The remarkable thing about these findings are that in addition to habitat harshness explaining the variation in cognitive maps, maintenance of this variation seems to be reinforced by sexual selection in the chickadees, since female preference prevents admixture between populations (Croston et al. 2015). Food-caching chickadees provide a strong empirical example of local adaptation of the anatomy and behavior associated with cognitive maps in response to the environment.

Admittedly, food caching is a special case of cognitive foraging, and it may be inappropriate to broadly compare the spatial behavior of food caching animals to spatial memory use in other animals. As per Croston et al. (2015), food caching is a direct response to temporal variation in resources. Additionally, the food cachers themselves dictate the spatial distribution of the resources they will target in the future. Thus, any predictions about directionality one might make about food caching animals may not hold for other animals. Furthermore, food

caching chickadees are not an appropriate system to test large scale predictions about the relationships between landscape structures, travel, and memory. Climates across the globe are not as predictably seasonal as in temperate zones; and foraging often manifests in other modes of behavior outside of food-caching.

1.3.5 Predicting space use and foraging success

To better understand the conditions in which a cognitive map increases foraging success, we have to explore the alternative ways foraging success can be achieved. As previously discussed, foraging theory predicts that animals will forage economically (e.g. Emlen 1966; MacArthur & Pianka 1966; Schoener 1971; Charnov 1976; Pyke et al. 1984; Krebs 1978; Stephens & Krebs 1986). A considerable amount of work has gone into predicting how animals might prioritize various resources, how they should behave upon encountering these resources, the breadth of resources one should expect an animal to utilize, and how animals should manage their time (e.g. Emlen 1966; MacArthur & Pianka 1966; Charnov 1976; Krebs 1978; Pyke et al. 1984; Stephens & Krebs 1986). Before an animal can make any of these types of decisions it must actually locate these resources. Thus, success is sometimes reduced to simply locating resources in a time minimizing fashion (Stephens & Krebs 1986, Janson 2000). Given this operational definition of success, one can make predictions about how an animal might achieve foraging success as levels of information it and types of foraging environments vary (Janson 2000, Janson & Bryne 2007).

The Movement Ecology Paradigm (MEP) (Nathan et al. 2008) is a convenient context in which to frame and test these predictions. Under the MEP, an animal's movement track is said to be derived from four components: 1) the animal's internal state, defined as its intrinsic physiological, neurological, or psychological condition, dictating why to move; 2) the animals

motion capacity defined as morphological or biochemical traits, dictating how to move; 3) the animal's navigation capacity, defined as the cognitive or sensory mechanisms, dictating where to move; and 4) external factors, defined as biotic or abiotic environmental drivers of movement (Nathan et al. 2008). Thus, one can predict the composition of movement tracks (the sequence of starts, stops, and turns) resulting from the interaction of different internal states, navigation capacities, and external factors.

As previously discussed, some animals navigate in the absence of complex memory, either in a completely non-oriented way (Codling et al. 2008; Reynolds and Rhodes 2009) or via path integration (Gallistel 1989; Bennett 1996). Animals both with and without cognitive maps can exhibit simple forms of navigation such as path integration (Gallistel 1989; Bennett 1996). In fact, simple modes of movement are common in the animal kingdom relative to navigation via cognitive map, (Gallistel 1989; Bennett 1996). However, there are clearly cases where memory driven foraging confers an advantage over path integration and other simpler navigational modes. Comparing foraging outcomes when animals utilize versus do not utilize memory (i.e., forage randomly) can help us understand the conditions whereby incorporating memory into foraging decisions significantly and importantly improves foraging efficiency. Janson (2000) outlined a set of predictions for how animals with and without memory are expected to respond to their environment in regards to steps and turns. Under the MEP (Nathan et al. 2008), Janson's (2000) predictions can be reframed as distinct movement tracks in response to varying external factors, namely the distribution and regeneration of resources, and varying the navigational state, namely spatial memory vs. no spatial memory. Given a navigation capacity that is not based on spatial memory, Janson outlined the expectation for movement tracks resulting from four external factors: (a) resources are depleted; (b) resources are not depleted; (c) resources are

uniformly distributed; and (d) resources are patchily distributed. Given scenario (a), Janson predicted that individuals avoid revisiting patches before they have regenerated by moving linearly (Janson 2000). Given scenario (b), he predicted that random steps and turns are equally as efficient as any other search strategy (Janson 2000), presumably because there is not a cost to revisiting sites. Given scenario (c), subsequent resources should be farther apart from one another, so individuals will take longer steps and narrower turns (Janson 2000). Finally, given scenario (d), Janson (2000) predicted that encountering a resource predicts the presence of other nearby resources, so short step lengths and sharp turns are taken to stay nearby.

There is much independent theoretical support for Janson's (2000) predictions about random foragers. Janson cites Cody's (1971) model of finches, where motion is generated from a random walk process in an environment with depletable patches showing that turning is always likely to cause an animal to return to a previously visited patch. Similarly, Prasad et al. (2006) independently simulated search behavior derived from a correlated random walk with patch depletion, and found that there was a 77% success rate of encountering an undepleted patch. Both studies lend support to prediction: (a) Cody's (1971) work demonstrating theoretically and empirically the cost of turning given depletable patches; and (b) Prasad et al.'s (2006) simulation demonstrating the benefit of linear motion given depletable patches. Janson (2000) also cites Stillman and Sutherland (1990) as support for this prediction (b), where they simulated foraging outcomes with rapidly replenishing resources and found that varying turning had little to no effect on foraging success. Because searching modes with frequent turns or linear motion performed similarly, this confirms Cody's (1971) suggestion that that when resources replenish quickly foragers will be successful regardless of search strategy (Stillman & Sutherland 1990). Benhamou (2007) independently used simulations to compare foraging success when movement

is driven by a Lévy Walk process to an alternative in which movement is driven by a “classical” random walk. Lévy Walks have a step-length distribution with an infinite variance, and are therefore considered super diffusive (Reynolds and Rhodes 2009). In other words, Lévy Walks exhibit narrow turns and consist of randomly oriented straight line movements, with short movements alternating with long movements (Reynolds and Rhodes 2009). Classical random walks have a step-length distribution with a fixed variance, and result in tortuous paths that are with shorter step-lengths than Lévy Walks of the same overall length (Codling et al. 2008). Benhamou (2007) found that Lévy Walks outperformed classical random walks only when resources were uniformly distributed, while classical random walks were more efficient in patchy environments (Benhamou 2007). As predicted by scenario (c), the superdiffusive movement process performed better in a uniformly distributed, widely spaced foraging environment, and as predicted by scenario (d), the movement process with the shorter steps and more torturous path was the most efficient in a patchy environment. Janson’s (2000) assertion that encountering a resource predicts the presence of subsequent resources stems from work done by Hubbell (1979) on the dispersion of tropical trees. Hubbell (1979) reports that all sampled species exhibited either a clumped or random distribution. Thus, prediction (d) can be expected to hold at least in the case of arboreal species where the majority of the diet is composed of tropical trees.

Janson (2000) provided a useful set of expectations for what a randomly foraging animal’s behavior should look like, but at what point does it pay to stop foraging randomly? Fagan et al. (2017) examined foraging success in dynamic landscapes for animals whose movement aren’t completely random, but don’t rely on memory. In other words, they were interested in movement oriented by some stimulus away from the current position but within

some perceptual range (Fagan et al. 2017). The question is “Under what conditions does gathering non-local information improve foraging success?” (Fagan et al. 2017). Using integrodifferential equations they constructed a movement model addressing how foraging success changes with variation in the perceptual range, the strength of the reaction to information, and the resource distribution (Fagan et al. 2017). Foraging success was defined as the animal’s ability to overlap in time and space with its resources (Fagan et al. 2017). The implication is that overlap would translate to use in terms of real world behavior. Landscapes were modeled as: 1) temporally static landscapes (i.e.; resource availability does not vary in time); 2) landscapes where resources are temporally pulsed (simulating some sort of periodic temporal availability or seasonality); 3) landscapes where the pulse is faster; 4) landscapes where resources are pulsed and spatiotemporally offset, (i.e., resource availability is variable in both time and space); and 4) temporally pulsed where patches are discrete with hard edges and therefore difficult to find (i.e., a discrete resource such as a tree rather than a patch where the patch boundary gradually dissipates) (Fagan et al. 2017). Fagan et al. (2017) found that when movement is based only on local information, foraging success is highest in temporally static landscapes, and decreases as landscapes get more complex. Foraging success was highest within a given landscape with zero outside information (Fagan et al. 2017). An example of such a landscape may be one where resource renewal is so fast that resource availability does not vary temporally, however real world examples of such landscapes are rare. When the animal is able to react to non-local information, then foraging success increased with the animal’s ability to quickly react to outside information (Fagan et al. 2017). Furthermore, the faster an animal was able to react to non-local information, the larger of a perceptual range it could take advantage of (Fagan et al. 2017). The increase in foraging success with an increased perceptual range is the

most dramatic when resources are difficult to find (Fagan et al. 2017). Fagan et al. (2017) conclude that gathering non-local information is useful in temporally dynamic environments with difficult to find resources patches when animals can react quickly to resources (Fagan et al. (2017).

In the case of cognitive maps, there is substantial added complexity which makes prediction and distinction challenging. Since cognitive maps are thought to facilitate goal directed behavior, one simple prediction that can be made is that goal directed movement should be efficient and directed, and consist of straight lines punctuated by sharp turns at target locations (Janson and Byrne 2007). However, this prediction is unsatisfying because there are cases where this pattern may be produced by simpler cognitive processes. Janson and Byrne (2007) stipulate that the way to determine if tracks of this nature are generated by cognitive maps is to check that the distance between the two points is greater than the animal's perceptual range. If this is the case, then the animal must have had prior information about the location of the goal (Janson and Byrne 2007). Unfortunately, if these data or a reasonable proxy are not available, distinguishing the underlying process generating the path is not possible.

Another prediction is that speed can be an indication of goal directed behavior, and by extension spatial memory (Janmaat et al. 2006; Janson and Byrne 2007). If increases in speed occur en route to a goal, and the increase in speed occurred outside of the animal's perceptual range, then spatial memory may be inferred because speed should represent the animal's anticipation of the value of the goal (Janmaat et al. 2006; Janson and Byrne 2007).

Unfortunately, the utility of this prediction is also dependent on the ability to obtain data on the perceptual range of the animal.

Predicting the sequence of resources an animal with spatial memory is likely to visit is also difficult because there are a number of decisions that can be made to maximize net energy intake or minimize search and travel time. If the foraging goal is to maximize total energy consumption, animals would be expected to target only the most valuable or profitable items (Janson 2000; Janson and Byrne 2007). Alternatively, net energy expenditure might be minimized by minimizing travel time between patches (Janson and Byrne 2007). This can be accomplished either by following a nearest neighbor rule, where the animal always navigates in a straight line to the nearest known available resource, or by following some sort of “look ahead” rule, whereby the animal chooses the optimal route between some subset of available resources before continuing on to the next subset (Janson 2000). Animals could also aim to minimize the overall travel path, and would have to do so amongst all resources outside the perceptual range (Altman 1974; Janson and Byrne 2007). In both cases the distance to the nearest neighboring goal should be greater than expected from a randomly searching forager, since remembered locations are, by definition, those be outside the animal’s current perceptual range (Janson and Byrne 2007).

Foragers may have multiple goals, such as social goals unrelated to foraging, or simultaneously maximizing energy consumption and minimizing travel distance. This makes prediction even more challenging, especially in cases where there is some tradeoff between distance to the next location and the value of that next location (Janson 2000). Janson (2000) however, proposes that if animals follow a look ahead rule, then both route optimization and target value may be taken into account by the forager. For example, if an animal looks N resources ahead, then as it is optimizing its route the between N-1 resources the highest valued resources should be driving the overall direction (Janson 2000).

Additionally, net energy may not be the only relevant currency. Nutritional ecologists take a multi-dimensional approach to studying an individual's nutritional goals, and have developed the Geometric Framework of Nutrition (GF) (Simpson & Raubenheimer, 2012). GF is simply a graphical way of representing and analyzing the nutritional composition of an individual's diet in multidimensional space, and provides quantitative tools for determining an animal's nutritional goals (Raubenheimer & Simpson, 1995). Simpson & Raubenheimer (2012) have experimentally demonstrated in a number of taxa that animals modulate their foraging behavior to maintain homeostasis, and that animals make foraging choices so that they achieve their target ratio of macronutrients. Since animals may modulate their behavior specifically in response to nutritional homeostasis, homeostatic goals should translate directly to foraging goals. If nutritional processes are operating at short timescales, then perhaps goal directed behavior can also be expected to happen over comparatively short timescales. In any case, if we consider foraging goals to be related to nutrient balancing instead of energy maximization, many of our predictions about space use could change.

Finally, if temporal data are encoded along with spatial information, then animals may behave such that recently depleted resources are avoided and only returned to when the resource is expected to replenish (Janson and Byrne 2007). Thus, animals should generally avoid recently visited locations (Janson and Byrne 2007).

1.3.6 Empirical studies on spatial memory in wild animals

Much of the initial empirical evidence for spatial memory in animals comes from experiments with captive animals. The advantages of captive experiments in this context are that they provide control over the perceptual range, previous experience with the relevant stimulus, and the availability of resources for the animal to detect (Janson 2000). Evidence from captive

chimpanzees (*Pan troglodytes*; Tinkelpaugh 1932; Menzel 1973), rhesus macaques (*Macaca mulatta*; Tinkelpaugh 1932), and yellow nosed monkeys (*Cercopithecus ascanius whitesidei*; MacDonald and Wilkie 1990), all demonstrate that primates are able to recall the locations of hidden rewards. When asked to relocate hidden rewards, each species chose efficient routes, generally adhering to a nearest neighbor rule (Tinkelpaugh 1932, Menzel 1973; MacDonald and Wilkie 1990; Gallistel and Cramer 1996). Evidence from captive vervet monkeys (*Chlorocebus pygerythrus*) indicates that vervets may follow a look ahead strategy and can look ahead up to three steps (Cramer 1995; Gallistel and Cramer 1996). Individual vervets were tasked with relocating experimentally hidden food rewards to see if they would choose the most optimal route. The actual routes taken by each monkey were compared to competing algorithms representing potential routes between each reward. The results of the experiment showed that vervet routes did not match the optimal (nearest-neighbor) algorithm, but were consistent with the algorithm representing a three step look ahead rule. Unfortunately, it is unclear whether the cognitive skills required in experimental settings are the same as those required for foraging across large landscapes, and there is even evidence that the ability to navigate across large spatial scales is developmental (Janson 2000). While Garber (1989) reports that wild tamarins (genus *Saguinus*) show evidence of spatial memory across large distances (average nearest neighbor distance reported as 148 meters), Menzel and Beck (2000) report that in closely related species of captive tamarins' the ability to orient themselves from their nest box was restricted to within 50 meters of the nest box. Data from captivity therefore seem to have limited utility, and we must be conservative about the inferences we make from such data.

Janson et al. (1997) and Janson (1998) studied spatial memory in wild capuchins (*Cebus apella*) through a series of field experiments, mitigating some of the aforementioned limitations

of captive experiments. They established an array of 15 feeding platforms throughout the study area during a period of fruit scarcity. This allowed them to manipulate the location, value, and renewal rate of the “resources” available to the capuchins (Janson et al, 1997; Janson 1998). Because the capuchins exhibited predictable and measureable changes in velocity and direction upon detecting feeding platforms, Janson et al. (1997) were able to estimate the food detection radius of the capuchins to be 82 meters with 95% confidence. Janson (1998) then monitored the capuchins’ spatial movements between the platforms, and compared them to the expected movement patterns under various models of random foraging. Janson (1998) found that the capuchins move in straight lines towards nearby feeding platforms more often than expected by random searching. Observed spatial patterns were only indistinguishable from random search models when the detection distance exceeded 225 meters (Janson 1998). Such detection distances were deemed highly unlikely due to the high degree of confidence in their detection estimates (Janson et al. 1997; Janson 1998). Janson (1998) explained that while these data provide good evidence for spatial memory in capuchins, they do not reveal if capuchins plan optimal routes. The data highlight the importance of knowing the perceptual range in studies of memory driven foraging, and show that it can be assessed experimentally.

Janmaat et al. (2006) addressed this topic in wild mangabeys (*Cercocebus atys atys*, and *Lophocebus albigena johnstoni*) by monitoring specific focal trees. They tested whether ranging patterns of the mangabeys was better explained by sensory cues or by spatial memory (Janmaat et al. 2006). The perceptual range (visual and olfactory) of the animals was assumed to be similar to those of humans due to their shared phylogeny (Janmaat et al. 2006). The tree species used was chosen because visual and olfactory detection of the fruit was deemed unlikely and few other species were known to eat the fruit (Janmaat et al. 2006). Janmaat et al. (2006) then

monitored the visitation patterns and approach speeds of the animals in response to variation in the fruiting state of the trees. They report that the likelihood of visiting a tree was significantly higher when fruit was available, was lower when trees recently fruited, and that the speed of approach varied significantly with the quality of fruit (Janmaat et al. 2006). Janmaat et al. (2006) argued that changes in behavior occurred outside the perceptual range and therefore indicate that mangabeys use past experience to anticipate changes in food quality and quantity.

Cunningham and Janson (2007) monitored the foraging behavior of white-faced saki monkeys (*Pithecia pithecia*) during a period of fruit abundance. Using nearest neighbor travel and site revisitation as indicators of spatial memory, they tested observed behavior against two models of random foraging. They found that the distance traveled between resources was four times greater than expected at random, and that the odds of visiting a resource increased greatly if the tree was very productive and recently visited (Cunningham and Janson (2007)). They also found that amongst preferred trees, sakis consistently chose the nearest of those trees (Cunningham and Janson 2007). Cunningham and Janson (2007) argued that the sakis' foraging decisions indicate both spatial knowledge of resources, and recent memory of food quality and availability. The use of recent experience to inform the animals about the quality of nearby resources, paired with bypassing certain resources for the highly productive resources are interpreted by Janson and Byrne (2007) as evidence of goal directed spatial behavior.

Interestingly, Cunningham and Janson (2013) monitored the same group of animals during a subsequent period of fruit scarcity, and found that movement patterns of the group no longer indicated any of the previous signs of memory. They suggest that the lack of high quality resources corresponds with the switch to a memoryless search strategy, and argue that spatial memory might be a mechanism allowing travel to rich and distant resources (Cunningham and

Janson 2013). In other words, goal directed behavior will only be exhibited when goals are available. If goals are not available, individuals may revert to simpler strategies. At the very least their results indicate behavioral flexibility in the face of dynamic landscapes, and show that a species can switch between multiple movement strategies under certain circumstances.

Avgar et al. (2015) studied memory and movement in caribou to test whether caribou (*Rangifer tarandus caribou*) movement was predicted by resource abundance, the density of predators, or the density of conspecifics (Avgar et al. 2015). Rather than examining step lengths and turn angles like the previously discussed studies, Avgar et al. (2015) constructed a spatially explicit cognitive movement model where an individual moves through a gridded landscape, and each movement decision is probabilistic and driven by what the individual knows about each cell in the grid. Sensory information and spatial memory are built into the model such that there is a decay rate associated with both memory and the perceptual range of the individual (Avgar et al. 2015). The model was parameterized such that three null hypotheses were considered: no non-local sensory input, memory decay, and no memory retention (Avgar et al. 2015). The model was then evaluated on its ability to predict the observed ranging data of the caribou (Avgar et al. 2015). Avgar et al. (2015) report that resource abundance was a strong predictor of caribou movement behavior, and that only for some individuals did the density of predators or other caribou have an effect. No individuals revealed patterns consistent with the null model of no sensory perception, but all individuals converged on the null model representing an “everlasting memory” characterized by no decay (Avgar et al. 2015). The results of their study suggest that caribou movement is in response to food, that caribou rely very little on sensory information, and that they rely heavily on long term spatial memory to make informed movement decisions (Avgar et al. 2015).

1.3.7 Study System

Current orangutan distributions are restricted to the forests of Borneo and Sumatra (Husson et al., 2009). They are rare or absent at high altitudes, and are most commonly found in lowland Dipterocarp forests, peat swamp forests, freshwater swamps and alluvial forests (Husson et al., 2009). Bornean and Sumatran forests are comprised of a large proportion of trees in the family Dipterocarpaceae. This causes extreme temporal seasonality, due in large part to the supra-annual mast fruiting exhibited by this family (Marshall et al., 2009; Wich et al. 2009). Forests with fewer Dipterocarp trees exhibit less extreme temporal seasonality, and orangutan densities are inversely related to the density of Dipterocarp trees (Marshall et al., 2009).

Orangutans are among the most highly encephalized of the non-human primates, in addition to having one of the slowest life-histories of any terrestrial mammal (Leutenegger, 1973; Harvey et al., 1987; Marino, 1998; van Noordwijk and van Schaik, 2005) They have fruit dominated diets (van Schaik et al., 1996, Leighton, 1993), and exhibit an extended developmental period where the young remain dependent on the mother to develop sufficient foraging skills (Schuppli et al., 2016). Furthermore, orangutans have been shown to use the lowest amount of energy per body mass of any primate (Pontzer et al. 2010).

It has been shown that diet is a major selective force driving the evolution of brain size (Benson-Amram et al., 2016; DeCasien et al., 2017; Holekamp and Benson-Amram, 2017). The large brain, coupled with the slow metabolism and slow life-history of orangutans indicate a strong evolutionary response to the extreme seasonality exhibited by Southeast Asian forests. Orangutans are clearly cognitively and physiologically adapted for the acquisition of spatially fixed, but temporally variable resources, making them an ideal model system for studying cognitive foraging in the wild.

Furthermore, in group living species, where individuals vary in their goals, group members follow decision making rules resulting in a compromise allowing the group to move as a cohesive unit. Groups typically follow a majority rule, where the resulting direction of the group is the average directional vector of all the individuals (Couzin et al., 2005; Strandburg-Peshkin et al., 2015). This makes studying resource selection and goal directed foraging difficult, since the resulting group level decision will not necessarily reflect the foraging goals of each individual. Orangutans, on the other hand, are semi-solitary (van Schaik et al., 1996), so most decisions can be interpreted as a true decision and an uncompromised goal. This makes orangutans a preferable model over other large brained primates in this context.

Sumatran forests have a lower stem density of Dipterocarp trees than their Bornean analogs, exhibit fewer periods of fruit scarcity, and shorter durations of scarcity periods (Marshall et al., 2009). Sumatran forests are therefore more productive than Bornean forests, and are considered more suitable habitats for orangutans (Marshall et al., 2009; Wich et al. 2009). As previously discussed, Croston et al. (2015) demonstrated that the intensity of the scarcity periods predicts the reliance on spatial cognition in chickadees. It follows that orangutans follow the same pattern, and therefore it seems likely that selection for reliance on spatial memory should be stronger on Borneo than on Sumatra. For this reason, the present study focused Bornean orangutans (*Pongo pygmaeus wurmbii*) at the Tuanan Orangutan Research Station (TORP).

1.3.8 Study site and population

The Tuanan study site (02° 09'06''S; 114° 26'26''E) was established in January 2003 within the 3,090 km² Mawas Conservation Area in Central Kalimantan, Indonesia (van Schaik et al. 2005). Tuanan is a peat swamp forest that comprises a 1137ha gridded trail system. It is 1.7 km east of the Kapuas River. Nearest to the river, the substrate consists of white sand on mineral

soil. With a rapid eastwardly transition to a peat substrate. Within the grid system, peat depth ranges from 0.5-2m and gets increasingly deeper further east outside the bounds of the study area. The site is a recovering forest, with a history of logging in the early 1990's, followed by low levels of local logging (van Schaik et al.2005). Orangutan density at Tuanan is among the highest in Borneo (Husson et al., 2009), with estimates ranging from 4.3-4.5 individuals/km² (van Schaik et al., 2005; Husson et al., 2009; Vogel et al., 2017).

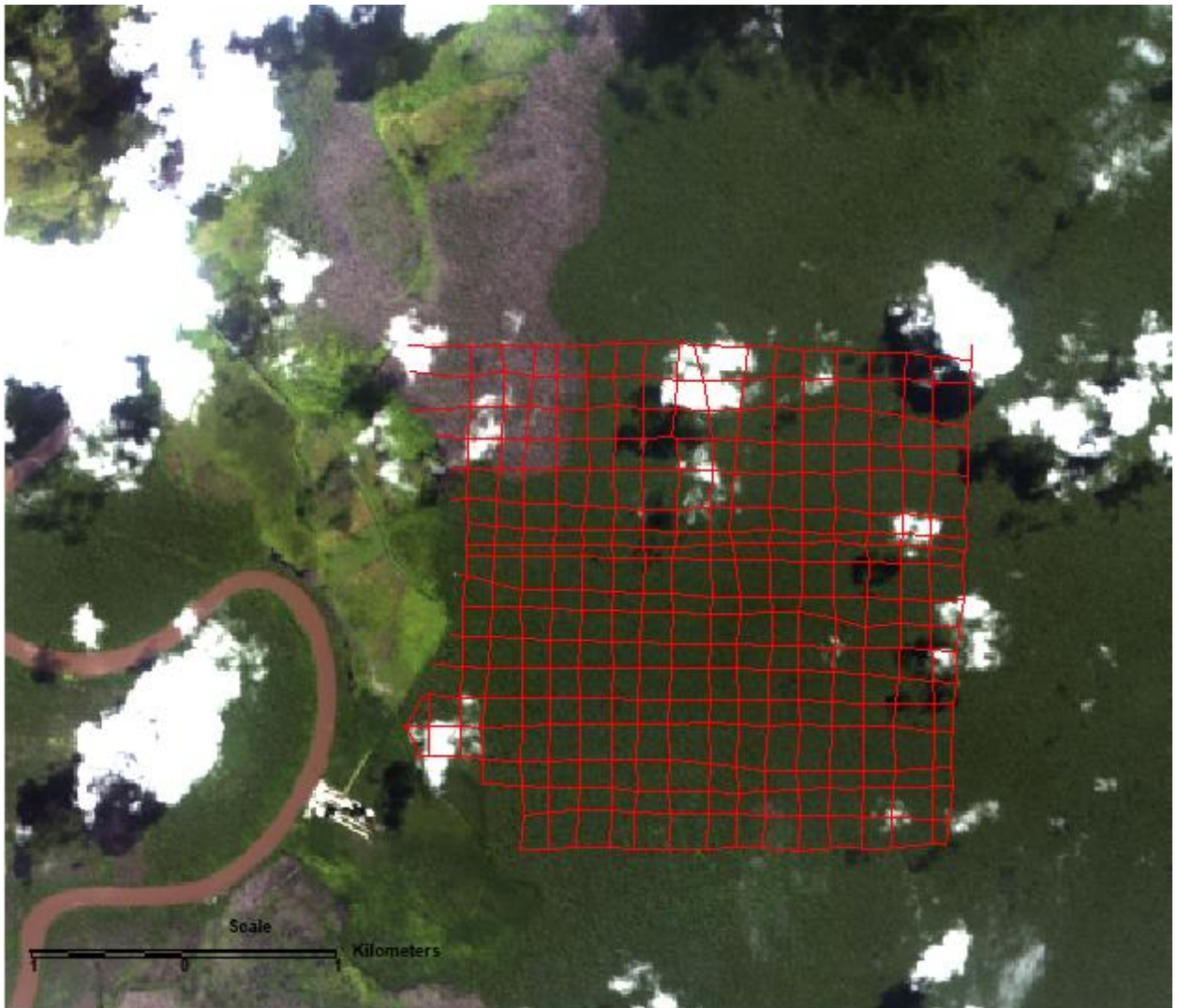


Figure 1.1 Map of the Tuanan grid system

Figures 1.2a and 1.2b show mean monthly rainfall and daily temperature respectively. Average daily temperature is 25.8°C ($\sigma = 3.05$), and average annual rainfall is 7.73mm/year ($\sigma = 2.3$). There is substantial monthly variation in tree phenology patterns at Tuanan (Figure 1.3), however fruit availability stays consistently low with the average percentage of fruiting trees per month being 4.61%.

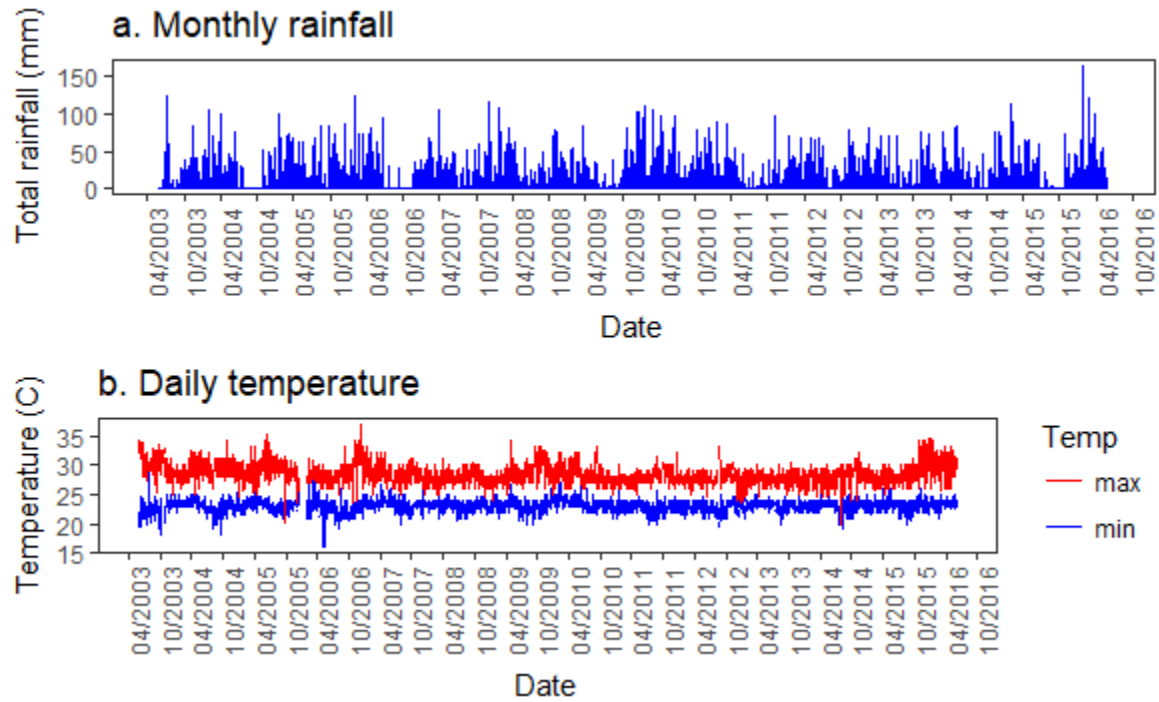


Figure 1.2 a) Total monthly rainfall in mm. b) Daily temperature in degrees Celsius. Red is the daily high, blue is the daily low.

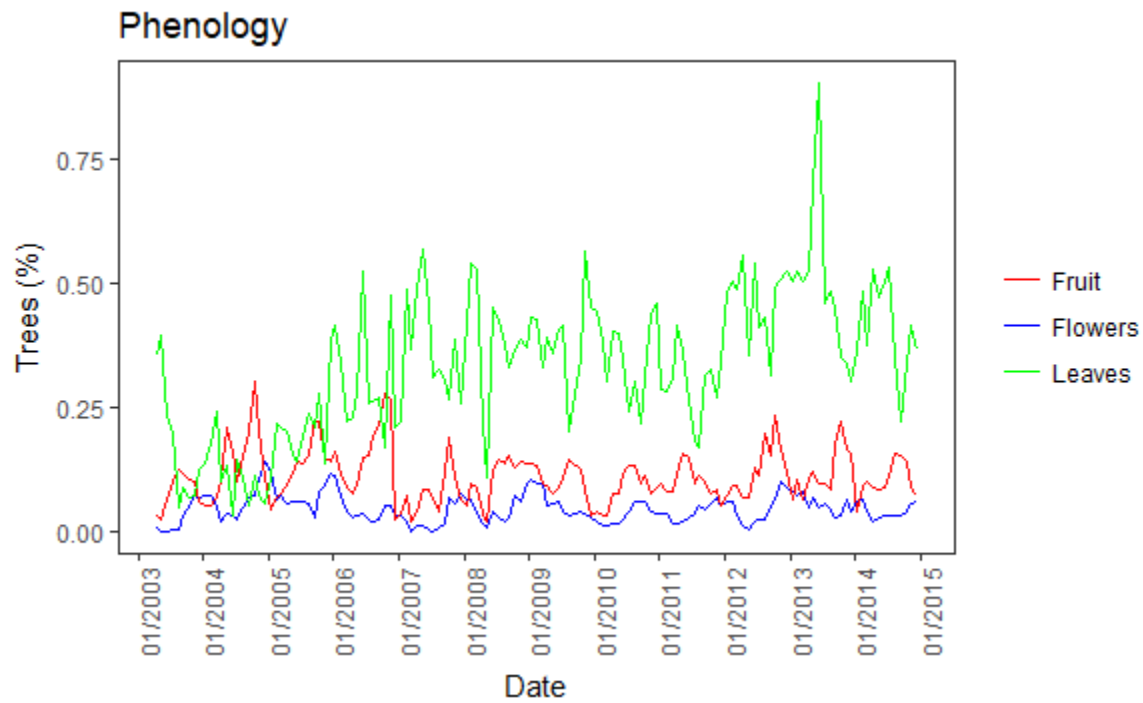


Figure 1.3 Monthly fruit availability index. Units are in percentage of trees. Red is percentage of fruiting trees, blue is percentage of flowering trees, and green is percentage of trees exhibiting young leaf flushing.

Knowledge of the orangutan diet at Tuanan is mostly complete, with the total number of known food items leveling off after about ten years of data (Figure 1.4). 82% of the known diet items have been analyzed for macronutrient composition.

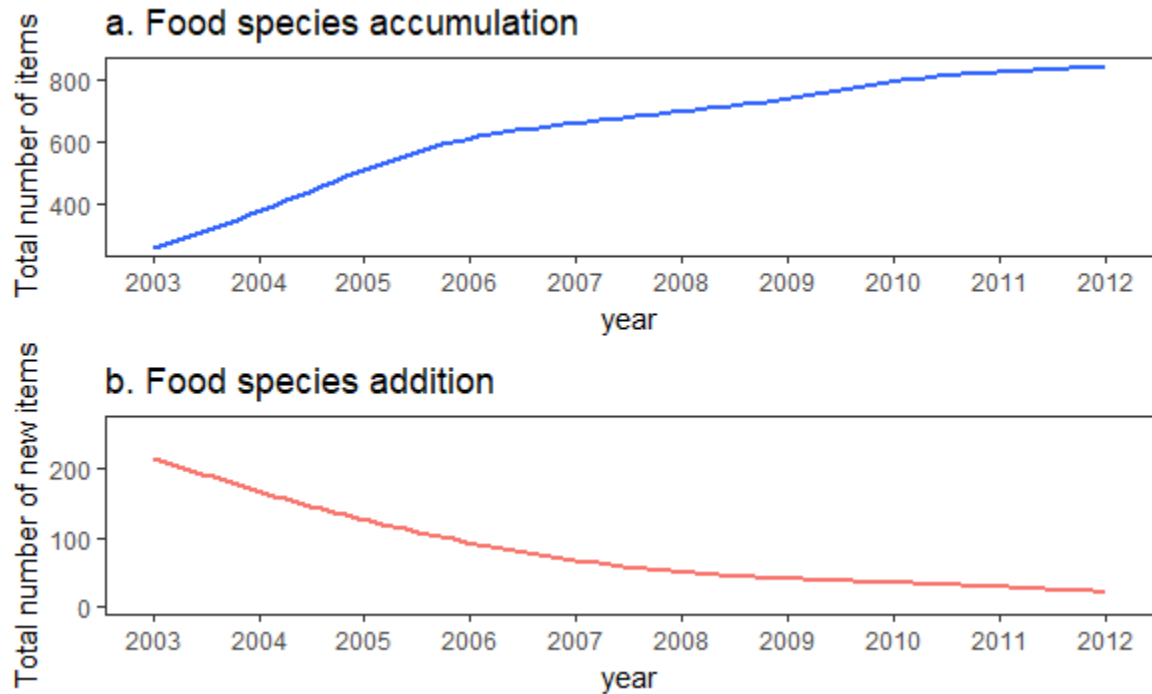


Figure 1.4 Accumulation curves and addition curves. a) is the total number of food items observed in the diet at each year. b) The total number of new food items added to the diet each year. The diet starts to stabilize after 9 years.

Orangutan behavioral data were collected using standard protocols

(<http://www.aim.uzh.ch/de/research/orangutannetwork/sfm.html>), and only data from full nest-to-nest focal follows were included in all analyses. For this study, 150 nest-to-nest follows were conducted on five main focal adult females (referred to as ‘focal’ individuals). Ten consecutive follow days at a time were attempted for each individual, with five being the minimum number of follows required. Data collection began in June 2014, and concluded in August 2015. Activity, ranging, and feeding data were collected using two minute instantaneous samples. During each feeding bout, food species, food part, ripeness, intake rate, and bout duration were recorded. Ranging data consisted of two minute GPS coordinates collected using handheld Garmin GPSMAP units. In addition to the focal individuals, full day, nest-to-nest follows were also

conducted on non-focal individuals opportunistically (Table 1.1). Activity, feeding, and ranging data were collected as previously described and ranging data were collected every thirty minutes.

All data were added to the larger behavioral database consisting of data collected since 2003. All behavioral data from 2003-2015 are described in detail in Vogel et al. (2017).

Table 1.1 Meta-data for all orangutans used in the analyses for this dissertation. Only individuals whose IDs are reliable and where full focal follows were completed are included. Asterisks indicate focal animals. All other animals were opportunistically sampled.

Orangutan name	Age class	Date First seen	Known birthdate	Estimated birthdate
Jinak*	Adult female with dependent	7/5/2003		1953
Juni*	Adult female with dependent	7/16/2003		1994
Kerry*	Adult female with dependent	7/28/2003		
Kondor*	Adult female			Jan-99
Milo*	Adult female	7/13/2003		2001
Danum	Immature male	9/27/2010		Jul-10
Dayak	Adult flanged male	10/3/2003		
Deri	Immature male	9/18/2004		Jul/Aug-04
Desy	Adult female	12/1/2003		
Ekko	Adult flanged male	3/21/2004		
Frodo	Adult unflanged male	5/18/2007		
Gismo	Adult flanged male	4/8/2004		
Helium	Adult flanged male	9/8/2012		
Henk	Adult flanged male	3/27/2004		
Jerry	Immature male	7/5/2003		Jun-17
Jimi	Adult flanged male	8/29/2005		
Jip	Immature male	2/10/2006	2/10/2006	
Joya	Immature male	10/10/2011		Jun /Jul-11
Katmandun	Adult flanged male	9/24/2011		
Kay	Adult flanged male	3/20/2005		
Kentung	Adult flanged male	1/10/2005		
Kino	Immature male	1/8/2007		Jan-07
Leo	Adult flanged male	3/30/2006		
Mawas	Immature female	7/21/2008	7/15/2008	8-Jul
Mindy	Adult female	7/13/2003		
Momo	Adult unflanged male	12/1/2009		

Nanio	Immature male	9/18/2004		1997
Niko	Adult flanged male	7/17/2003		
Otto	Adult flanged male	8/3/2008		
Pinky	Adult female	10/9/2008		
Preman	Adult unflanged male	9/11/2003		
Rambo	Adult flanged male	7/15/2003		
Sidony	Adult female	9/27/2007		
Sony	Immature male	3/28/2010	3/28/2010	2010
Streisel	Immature female	9/27/2007		2002
Sumi	Adult female	7/28/2003		
Talia	Adult female			
Ted	Adult unflanged male			
Tomi	Adult flanged male			
Vini	Adult unflanged male	5/22/2012		
Wodan	Adult unflanged male	4/27/2004		

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Chapter 2. Variation in spatial movement as it relates to nutritional balancing in Bornean orangutans (*Pongo pygmaeus wurmbii*)

2.1. Introduction

The optimal foraging literature has been instrumental to our understanding of animal energy budgets and the evolution of decision making (Charnov, 1976; Pyke, 1984; Krebs, 1978; Bateson & Kacelnik, 1998). The reality that both time and energy are constraints on behavior has led to work on predicting how these constraints dictate choices about the what, where, and how of resource acquisition (Pyke et al., 1977). The presumption is that selection favors individuals that optimize their decisions, usually through risk minimization and energy maximization.

Energy has long been the predominant currency through which optimal foraging and evolution are studied. Dietary categories have historically been framed around categorical differences in the energy content of foods, and deciding between high and low energy foods has been invoked as a means of niche partitioning in animal communities (Bell, 1971; Jarman, 1974; Kay, 1975; Owen-Smith, 1988; Codron et al., 2007; Shipley, 2007). Even fine-scale foraging decisions such as optimal patch choice are modeled in terms of diminishing energetic returns (Charnov, 1976). Although the foraging literature has been heavily calorie-centric, there has been a recent and growing shift towards acknowledging the importance of other nutritional currencies.

Some of the earliest work that explicitly addressed the role of nutrients in diet optimization came from the linear programming and ungulate literature. This literature demonstrated that animals attempt to optimize nutrient intake relative to plant secondary compounds, and showed that certain micronutrients can be extremely limiting for animals

(Freeland & Jansen, 1974; Westoby, 1974; Belovsky, 1978; Belovsky, 1981). This research influenced Milton's (1979) work on the feeding ecology of folivorous primates, where she suggested that they optimize their diets by targeting a specific ratio of protein to fiber.

McNaughton (1988) showed that the spatial distribution of mineral nutrients predicted ungulate density, and forest level experiments by Ball et al. (2000) showed that experimentally increasing the nitrogen content (i.e., quality) of leaves caused an aggregate response in mammal presence. Furthermore, recent work on invertebrates has shown that they have marked responses to nutrient availability, demonstrating both changes in invertebrate distribution and dietary strategy due to micronutrient limitation (Kaspari et al., 2014; Kaspari et al., 2016; Clay et al., 2017).

Advances in our understanding of stable isotopes and their relationship to diet and nutrition have changed how we view trophic dynamics and niche differentiation (Newsome et al., 2007; Fernandes et al., 2012). Now it is not only possible to reconstruct diets, but isotopic niche space can be further translated into nutritional niche space, allowing us to move beyond the classical tropes of high and low energy strategies. Furthermore, is it now clear that different types of nutrients interact with genes in a number of measurable ways, and that there are clear, biologically meaningful reasons to optimize behavior with regards to nutrient intake (Reitsema, 2013; Minihane, 2015). There is even evidence that some micronutrient regulated processes are important enough that "triage" mechanisms have evolved to conserve those processes in the short term at the expense of long term health (Ames, 2006; McCann & Ames, 2009).

Simpson & Raubenheimer (2012) maintain that because adequate nutrition is fundamental to cell maintenance and growth, natural selection should optimize foraging in such a way that individuals are always able to meet their nutritional demands. They maintain that species should have a specific balance of macronutrients as their target, and that individuals

should modulate their feeding behavior specifically to achieve that nutritional balance (Simpson & Raubenheimer, 2012). They developed the *geometric framework of nutrition*, which allows us to visualize and analyze how individuals' nutritional intake actually fluctuates. This framework was used to show that spider monkeys (Felton et al., 2009) and gorillas (Rothman et al., 2011) have taxon specific nutrient targets, and switch between a diverse set of available food items, consistently hitting their respective targets.

Experimental work using this framework has been compelling, however field measures of nutritional targets are assumed to be biologically relevant without a clear means of verification. How much of the daily balance of nutrients that wild individuals achieve is just a function of the environment, and not a true target? Even when total calories are the currency of interest, it can be difficult to predict foraging decisions since both the interpretation of the goals, and assumptions about the distribution of relevant food items might be different than what the animals actually experience (Vogel & Janson, 2011). If the observed balance of nutrients in wild populations are in fact biologically relevant targets, then the ratio of nutrients should be different than chance would predict, and there should be evidence of goal directed behavior in response to nutrients.

The spatial and temporal distribution of food is the most fundamental and immediate constraint on an individual's ability to forage (Krebs 1974; Pyke et al. 1977). Before energy or nutrient intake occurs, those resources containing the nutrients must be located. There is substantial literature on how search and navigation strategies can vary, and what conditions might exert selection pressures for the different movement strategies (e.g. Stephens & Krebs, 1986; Janson, 2000; Janson & Bryne, 2007; Nathan et al., 2008). Most notably, it is possible to distinguish between random search strategies, and goal directed behavior (Janson, 2000; Hill, 2006; Janson & Bryne, 2007; Nathan et al., 2008).

Completely random searching is un-oriented, and consists of uncorrelated changes in direction and velocity (Reynolds and Rhodes, 2009). Goal directed motion is typically described as some form of area restricted search (ARS), with the predictions about direction and velocity depending on the amount of information stored by the forager (Janson, 2000; Hill, 2006; Janson & Byrne, 2007). If an animal is not relying on prior knowledge about the location of resources, then its motion is expected to consist of an increase in sharp, slow, correlated turns upon encountering a resource patch. This allows it to have sufficiently tortuous motion to keep it within the bounds of the patch (Viswanathan et al., 1999; Fauchald & Tveraa, 2003; Hill, 2006; Viswanathan et al., 2008; Dragon et al., 2012). As the time since the last resource encounter gets longer, motion becomes more linear and the animal is expected leave the patch to locate another one (Viswanathan et al., 1999; Fauchald & Tveraa, 2003; Hill, 2006; Viswanathan et al., 2008; Dragon et al., 2012). If an animal is using non-local information to locate resources, then motion is expected to be linear and directed (autocorrelated), and always in the direction of a goal (Janson, 2000; Janson & Byrne, 2007). When animals rely on memory, then the distance between goals should be farther than the perceptual range of the individual, and sharp changes in direction are expected to only be from one goal resource towards another goal resource (Janson, 2000; Janson & Byrne, 2007). Velocity is also expected to increase when an animal moves in the direction of a highly valued goal. Increases in velocity occurring beyond the perceptual range can signal a change in behavior in anticipation of the goal due to prior information about that goal (Pochron, 2001, Janson & DiBitetti, 1997, Janmaat, 2006).

If the observed ratio of macronutrients in wild populations is a true target, then changes in direction and velocity should vary significantly with the observed nutritional trajectory (i.e., change in distance in nutritional space from the target ratio over time). If an animal is searching

randomly, then there should be no relationship between that animal's movement parameters and its nutritional trajectory. If the animal is using ARS, then it should exhibit low velocity with increased turning if the animal is near its nutritional target. Movement becomes linear once the animal leaves the resource. If the animal is using memory or other non-local information, then velocity should be high and autocorrelated, and turning should be high, but not necessarily autocorrelated, when the animal is near its nutritional target. By examining nutritional balancing and motion parameters independent of actual food items and actual locations, we are not at risk of misidentifying goals or mischaracterizing the animal's perception of resource distributions. We can objectively evaluate whether the suspected desired outcome of the foraging day (i.e., the target ratio of nutrients) actually corresponds to goal directed behavior and the animal's search strategy.

Hypothesis 2.1a: Macronutrient balancing by orangutans is not a function of random food acquisition and represents a biologically relevant outcome of foraging.

Prediction 2.1a: The mean daily ratio of macronutrients for the population is not an arbitrary metric and represents a nutritional target. The empirical population mean is expected to be significantly different from population means derived from random feeding simulations.

Hypothesis 2.1b: Alternatively, the empirical population mean could simply reflect the average macronutrient ratio of known orangutan food items.

Prediction 2.1b: In this case, the empirical mean should not be significantly different from the mean of random feeding simulations.

Hypothesis 2.2a: The mean macronutrient ratio is a biologically meaningful foraging goal, and individuals make spatial decisions that facilitate macronutrient balancing.

Prediction 2.2a: Deviations from the nutritional target (in nutritional cartesian space) vary in response to changes in the diagnostic features of orangutan movement tracks (in physical space), with motion parameters indicating non-random motion when near the target.

Hypothesis 2.2b: Alternatively, nutritional balancing may not be an important foraging goal, and spatial behavior may be unrelated to macronutrient ratios.

Prediction 2.2b: In this case, motion parameters will not be statistically associated with the distance from the nutritional target, and indicate a random movement strategy whereby spatial decisions are independent of dietary decisions.

2.2. Methods

2.2.1 Study site and system

Data were collected at the Tuanan Orangutan Research Station in Central Kalimantan, Indonesia. Tuanan is a peat-swamp forest that comprises about 1137 ha, with peat depth typically ranging from 0.5-2 m. Orangutan density at Tuanan is among the highest in Borneo (Husson et al., 2009), with estimates ranging from 4.3-4.5 individuals/km² (van Schaik et al., 2005; Husson et al., 2009; Vogel et al., 2017).

2.2.2 Behavioral data collection

Orangutan behavioral data were collected using standard protocols (<http://www.aim.uzh.ch/de/research/orangutannetwork/sfm.html>), and only data from full nest-to-nest focal follows were included in this analysis. For all focal animals, activity, ranging, and feeding data were collected using two-minute instantaneous samples. For this study, in addition to the regular project data collection, 150 nest-to-nest follows were conducted on five focal adult

females. Females were chosen based on level of habituation and ease of relocation. Focal females are described in Table 2.1. Females were followed for a minimum of five consecutive days. Females were opportunistically followed for an additional five days when possible, with ten days being the maximum number of consecutive follows permitted by the research station. Data were collected between June 2014 and August 2015. During each feeding bout, food species, food part, ripeness, intake rate, and bout duration were recorded. Ranging data consisted of two-minute GPS coordinates collected using handheld Garmin GPSMAP units. For all non-focal individuals, nest-to-nest follows were conducted opportunistically. Activity, feeding, and ranging data were collected as previously described and ranging data were collected every thirty minutes. All data were added to the larger behavioral database consisting of data collected since 2003. All behavioral data from 2003-2015 are described in detail in Vogel et al. (2017). Nest-to-nest follows from this database, consisting of 42,482 follows of 37 individuals, were used in an analysis of simulation results (see section 2.2.4). Only data from focal females were used to analyze macronutrient intake and goal directed behavior (see section 2.2.5).

Table 2.1 Meta-data for focal female orangutans.

Orangutan name	Age class	Estimated birth year
Jinak	Adult female with dependent	1953
Juni	Adult female with dependent	1994
Kerry	Adult female with dependent	NA
Kondor	Adult female	1999
Milo	Adult female	2001

2.2.3 Nutrient intake

The macronutrient compositions of each food item were taken from the long-term Tuanan nutritional database. The database encompasses 82% of the known orangutan diet. The sample collection, preparation, and nutritional analysis of each food item are detailed in Vogel et al. (2017).

Protein (P) and non-protein (Npe) kcal intake were calculated per feeding bout per individual per day such that

$$P = l \times r \times e_p \quad (2.1a)$$

and

$$Npe = l \times r \times e_{Npe}. \quad (2.1b)$$

l is bout length, r is intake rate, and e is energy (in P or Npe). A feeding bout was defined as an event beginning when an individual first ingests a food resource and ends once it leaves that resource or switches to a different resource. Cumulative intake was calculated by summing intake across bouts. The ratio of non-protein energy (kcal) to energy from protein ($Npe:P$) per day was calculated for all individuals from 2003-2015 using the pooled data from the long-term Tuanan orangutan database. The cumulative ratio of macronutrients per day was calculated for all known individuals where nest to nest follows were successfully completed. Data spanned from 2003 to 2015. The mean ratio of macronutrients for the entire orangutan population was then calculated.

To test whether the mean ratio of $Npe:P_i$ is a function of chance or the average ratio of orangutan foods, orangutans were simulated to randomly feed under resource rich conditions using the following procedure: the empirical distribution parameter values were calculated for

the observed orangutan bout lengths, number of bouts per day, number of available food items per day, and number of food items eaten. These values were then used to parameterize the associated theoretical density functions for each variable. For each of 10,000 iterations, the available food items, food items eaten, bout lengths, and number of bouts per day were randomly drawn from each density function. Resource rich conditions were determined based on Food Availability Index (FAI) values from 2003 to 2015. FAI was binned into quantiles corresponding to high, medium, and low periods. High FAI periods were considered resource rich periods, and known food items consistently available during high FAI periods were designated as available foods and stored in a data frame. The nutritional database, comprised of 811 known food items, had 285 items commonly consumed during high FAI periods. The available foods data frame was then subset so that number of food items available to encounter was a random sample of the data frame drawn from the available food items theoretical density function.

2.2.4 Simulation

Table 2.2 Simulation parameter values

Foraging parameter	Distribution	μ
Number of bouts per day	Normal	$\mu=23.16, \sigma=10.03$
Number of food items eaten	Normal	$\mu=9.50, \sigma=3.52$
Number of food items available per day	Normal	$\mu=50.3, \sigma=25.6$
Bout length (min)	Exponential	$\lambda^{-1}=17.62$

Let d represent the food items eaten per simulated day, b represent the total number of bouts per day, and l represent bout length. Values for b and l are drawn from an exponential

density function (equation 2.2a), and values for d and b are drawn from the standard normal density function (equation 2.2b)

$$f(x, \lambda) = \lambda e^{-\lambda x} \quad (2.2a)$$

$$f(x|\mu, \sigma^2) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(x-\mu)^2}{2\sigma^2}} \quad (2.2b)$$

with the corresponding model terms represented in Table 2.2. The value for d is the number of food items to be randomly selected from the nutritional database at each iteration ($n = 10,000$ iterations).

$$Npe: P_i = \sum_i^n \left(\frac{\sum_j^{b_i} Npe_j}{\sum_j^{b_i} P_j} \right) \quad (2.3)$$

$$\sum_j^{b_i} Npe = l_j \times e_{Npej} \times r_j \quad (2.4a)$$

and

$$\sum_j^{b_i} P = l_j \times e_{Pj} \times r_j \times P_j \quad (2.4b)$$

where e is the energy (in P or Npe) in the patch randomly selected from d_i food items. Values for r and e are drawn from the nutritional database.

The simulated $Npe: P$ values represent the value of $Npe: P$ that an individual should end on each day if it is consuming food randomly. This simulation assumes nothing about search and navigation or dietary preference. To test if orangutans are balancing macronutrients in a non-random way, and to test if their ratio of $Npe: P$ is equal to the average $Npe: P$ ratio of orangutan food items, the simulated $Npe: P$ values were compared to the empirically derived $Npe: P$ values using the Wilcoxon rank sum test. Empirical and simulated $Npe: P$ values were also compared to

the $Npe:P$ of the food items themselves using the Kruskal Wallis rank sum test and multiple comparisons tests.

2.2.5 Goal directed behavior

To test whether the above ratio of $Npe:P$ can be interpreted as a nutritional goal, behavioral modification was examined in response to deviations around $Npe:P$ per foraging day.

The cumulative ratio (c) of $Npe:P$ at the end of each bout was calculated for each of the five focal females, and their cumulative trajectories (their changes in position in nutritional cartesian space relative to their target) were tracked for each day.

Formally,

$$(c_n)_{n=1}^b = \begin{cases} c(1) = \frac{Npe_1}{P_1} \\ c(n) = c(n-1) + \frac{Npe_n}{P_n} \end{cases} \quad (2.5)$$

At the end of each bout, the Euclidean distance from the target ratio (equation 2.6) was calculated. To do so, the mean ratio of the population (see Results, Hypothesis 2.1) was treated as the nutritional target rail, and thus the slope of a line given the formula $y = mx + B$. The perpendicular distance of each point to the target rail was then calculated, whereby

$$distance = \frac{|B+mx_0-y_0|}{\sqrt{(1+m)^2}} \quad (2.6)$$

To test for behavioral modulation in response to the distance from the target rail, structural changes in the orangutan's spatial behavior were analyzed using behavioral change-point analysis (BCPA) (Gurarie et al., 2009). BCPA is a likelihood-based method for detecting structural changes in a movement path. GPS tracks are modeled as stationary, continuous space - continuous time Gaussian processes. BCPA is advantageous over other behavioral segmentation

methods in that it is robust to unevenly sampled data and the movement variables are easily modeled by autoregressive time-series models (Gurarie et al., 2009).

Rather than handling absolute positions or compass bearings, estimated speeds and turning angles were decomposed into two orthogonal components.

$$V_p = V \sin \theta \quad (2.7a)$$

and

$$V_t = V \cos \theta \quad (2.7b)$$

V is displacement/time interval, and θ the turning angle (Gurarie et al., 2009). Speed, directional persistence, and variability are supposed to be captured in these two variables. V_p , named persistence velocity, is defined as the tendency of motion to persist in a given direction and the velocity of that motion. V_t , named turning velocity, is defined as the tendency of motion to head in a perpendicular direction in a given time interval. Each component possesses its own μ , σ , and ρ (Gurarie et al., 2009). These parameters are the diagnostic features of a movement track and make it easy to identify discrete modes of movement behavior.

Goal directed movement is defined as one of two scenarios. Informed search is any motion where V_p shows a high μ , σ , and ρ indicating faster and more directed motion with abrupt starts and stops, and where V_t shows a high σ and high ρ . Area Restricted Search (ARS) is any motion where V_p shows a low μ , high σ , and ρ indicating slow but correlated motion with abrupt starts and stops, and where V_t shows a high σ , and low ρ , indicating more tortuosity and a longer turning radii.

Table 2.3 Goal directed motion parameter expectations.

	V_p			V_t	
	μ	σ	ρ	σ	ρ
Area Restricted Search (ARS)	low	high	low	high	low
Informed search	high	high	high	high	high

Goal directed behavior was examined by testing how fluctuations in μ , σ , and ρ predict the Euclidean distance from the target rail in nutritional space using generalized additive mixed models (GAMM). When an animal is behaving in a goal directed way, it should be near it's nutritional target ratio. Other modes of movement should not translate to successfully achieving the target ratio. Thus, when the distance from the target is small, movement parameters should reflect either ARS or informed search as per Table 2.3.

GAMM were run using the MGCV package in R (R Development Core Team, 2017; Wood & Wood, 2017). GAMMs are semi-parametric extensions of generalized linear models where the linear predictor involves a sum of smooth functions of the predictor variables. Smooth terms are represented using penalized regression splines. Inference is based on these smooth functions (Hastie and Tibshirani, 1986, 1990; Wood, 2006a). For further information on how to calculate smooth functions, see Wood (2006b). GAMM is advantageous because of the relaxation on parametric assumptions, and because GAMM can reveal non-linear relationships in the data. Individual ID was included as a random effect in each model, and random slopes were included in the models to minimize type 1 errors. Thus, all models are fully maximal (Barr, Levy, Scheepers, & Tily, 2013).

2.3. Results

Hypothesis 2.1

Simulation outputs suggest that if an orangutan randomly feeds amongst the available food items at Tuanan, the resulting ratio of $Npe:P$ is equal to the mean $Npe:P$ for orangutan food items. The observed ratio of $Npe:P$ for orangutans was significantly lower than simulated $Npe:P$, and was significantly lower than the average ratio of $Npe:P$ for orangutan food items (Kruskal Wallis rank sum test, $p < 0.001$; multiple means comparison, $p < 0.05$; Table 2.4). There was not a significant difference between mean $Npe:P$ of orangutan foods and simulated $Npe:P$. These results support Prediction 2.1a of Hypothesis 2.1a, indicating that in nature orangutans are consuming more dietary protein than can be explained by random chance based on the random foraging simulation. Figure 2.1 shows the distribution of simulation outcomes and actual orangutan observations.

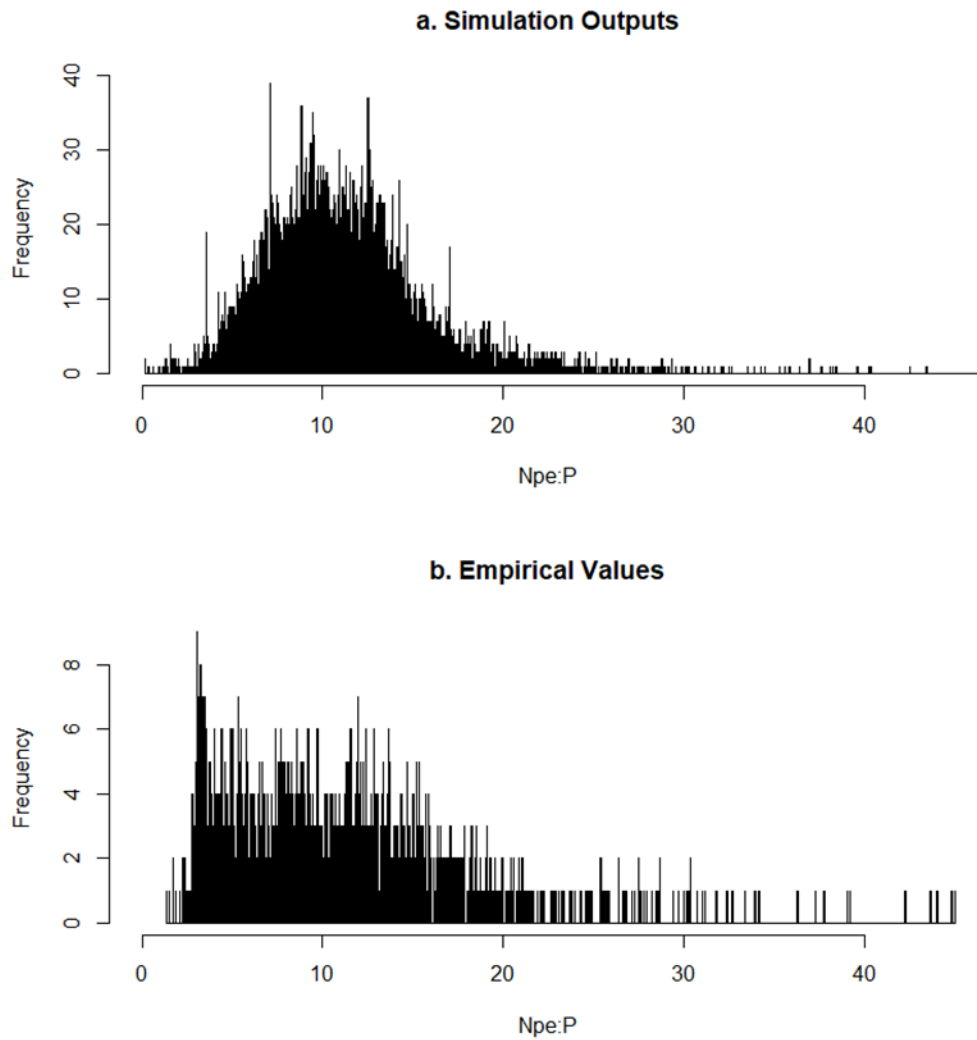


Figure 2.1 Empirical and simulated data: Histograms of a) simulated data after n=10,000 iterations, and b) empirically derived values of Npe: P. The x-axis represents the ratio of non-protein (kcal) to protein (kcal) at the end of a foraging day. The y-axis is the frequency with which each value of Npe: P is observed. Simulated ratios of Npe: P are significantly higher than observed values (Wilcoxon rank sum test, $p < 0.001$).

Table 2.4 Kruskal Wallis and multiple comparisons tests

Kruskall Wallis Rank Sum					
χ^2	df	p	Multiple Comparisons		
66.29	2	p < 0.001	Food Items-Orangutan*		
			Food Items-Simulation		
			Orangutan-Simulation*		
Dataset			Mean	Median	Mode
Orangutan food			14.26	10.98	4.21
Orangutan intake			10.58	9.63	14.69
Simulated intake			11.16	10.59	14.23

Results of a Kruskal Wallis test, a multiple comparisons test, and summary statistics about the three data sets are included here. Comparisons in italics and with an asterisk (*) are significantly different after Bonferroni correction

Results from the simulation support the notion that the observed ratio of $Npe:P$ for wild orangutans is not arbitrary. It could be that a 10.58 ratio of $Npe:P$ is a legitimate target balance of macronutrients, and that individuals make discrete foraging decisions to facilitate achieving this ratio of nutrients. If the nutritional composition of individual food items was similar across the known diet, one could infer that a ratio of 10.58 is an inevitable statistical artifact. The available diet at Tuanan however, is quite varied. Figure 2.2 illustrates this variability. Figure 2.2a explicitly represents the variability in all four macronutrients across all food items. The identity of each food item was purposely left out so as not to distract from the four-dimensional landscape. Carbohydrates are the most variable, followed by fiber, protein, and lipids. Figure 2.2b shows how the mean ratio of nutrients for each food item differs from each other and the

overall mean. These plots illustrate the multitude of ways an orangutan can switch between foods to obtain different ratios of macronutrients.

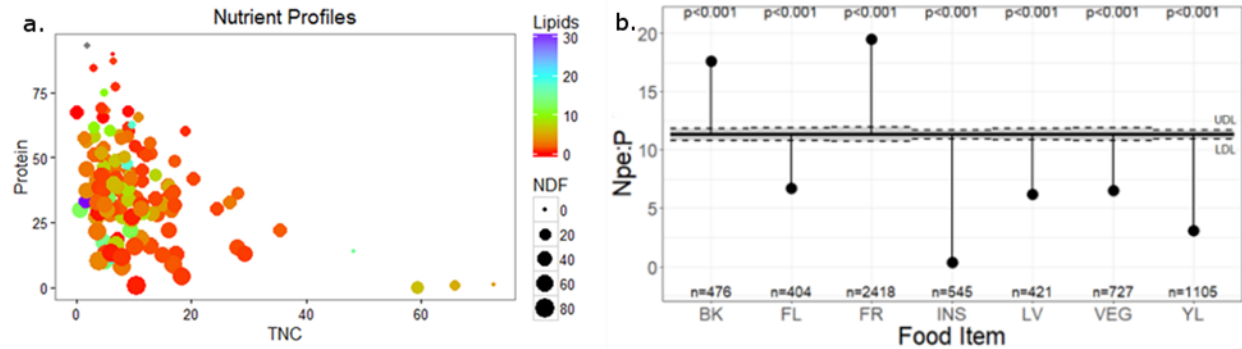


Figure 2.2 Macronutrient variability: a) A four-dimensional representation of the macronutrient profile of each item in the orangutan diet. Units are in kcal. The standard deviations are as follows: protein =7.2; carbohydrates =13.4; lipids=3.9; fiber=12.8. b) A non-parametric analysis of means illustrating the significant differences in $Npe:P$ between food types. n is the number of species in each category, p -values indicate significant differences from the grand mean. The grand mean is represented by the horizontal line connecting each category.

It is clear that the orangutan diet enables individuals to select and switch between resources during the foraging period such that they have some control over that ratio of $Npe:P$ they achieve by the end of their active period.

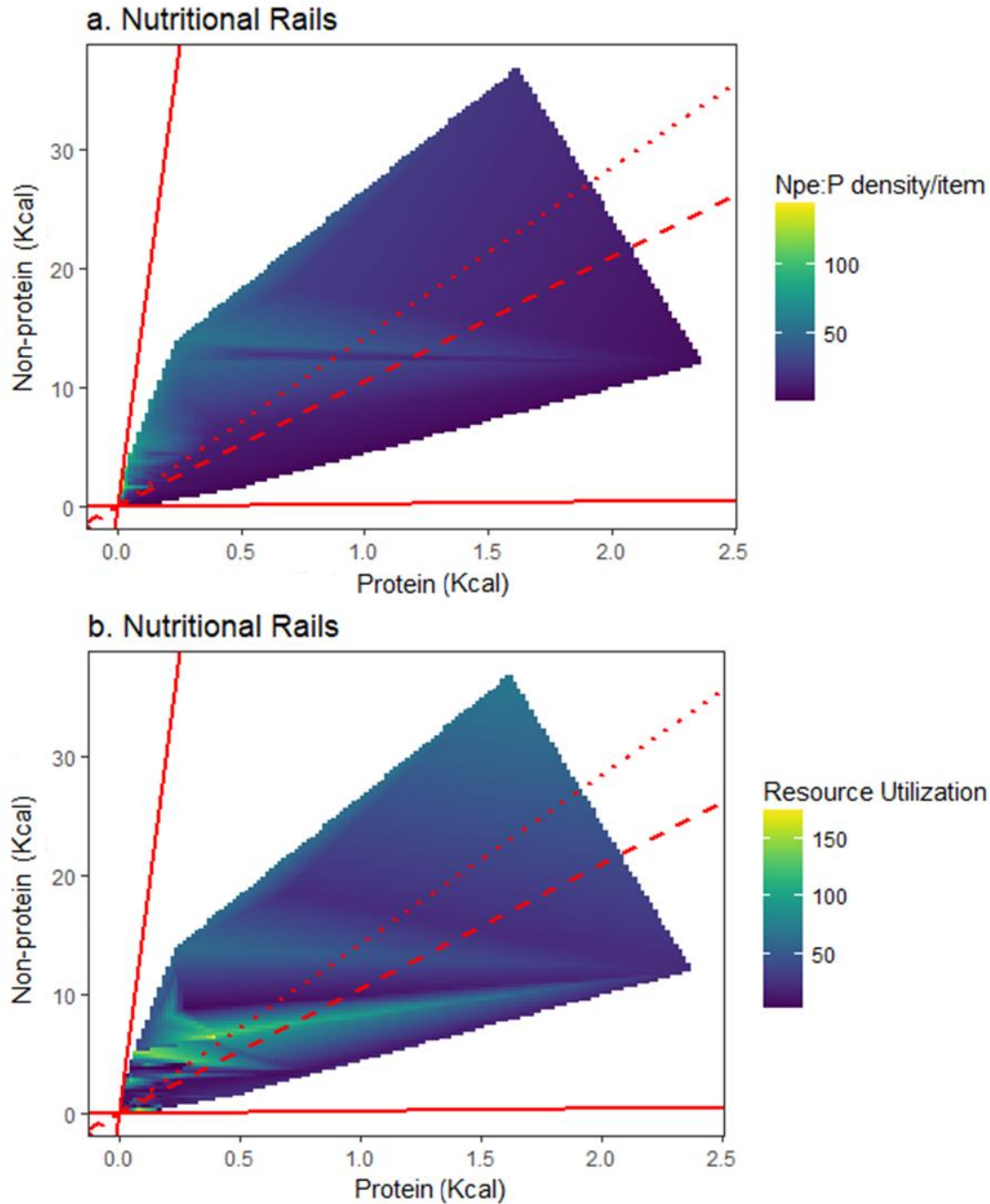


Figure 2.3 Nutritional target rails: The two outer rails represent the two possible extremes in terms of $Npe:P$ given the available food items. The dotted line is the average $Npe:P$ of the available food items, and the dashed line is the target $Npe:P$ of the orangutan population. In Figure 2.3a, the heatmap is an interpolation of the ratio of $Npe:P$ in each known food item in the diet. In Figure 2.3b, the heatmap is an interpolation of the total number of feeding bouts on each respective food item.

Figure 2.3 illustrates where the orangutan target rail falls in nutritional space relative to the items in the orangutan diet. The heatmap shows the relative shape of the entire diet breadth

on the nutritional landscape. The heatmap in Figure 2.3a characterizes how the relative proportions of protein (kcal) to non-protein (kcal) of food items vary across the extent of orangutans' nutritional space, and the heatmap in Figure 2.3b shows what parts of the nutritional landscape are most heavily utilized. It is apparent that regions in Figure 2.3a with low (blue) values of $Npe:P$ correspond to analogous bright (yellow) regions of Figure 2.3b. It seems that the orangutans invest a large amount of foraging effort in the proportionally protein rich parts of their nutrient space. Additionally, protein intake falls along a relatively horizontal line, potentially suggesting protein prioritization. The data represented in Figure 2.3 suggest that individuals may be making discrete choices explicitly related to the macronutrient composition of their available foods.

If a ratio of 10.58 $Npe:P$ is indeed an explicit foraging goal beyond net caloric gain, then individuals are expected to explicitly modulate their behavior to facilitate the acquisition of specific macronutrients. Figure 2.4 is a snapshot from one day of foraging from one adult female. As we monitored the cumulative intake of macronutrients, we recorded her trajectory in nutritional space in relation to the proposed target ratio of $Npe:P$. Each point represents the end of a feeding bout, and her new position in nutrient space given her latest additive consumption. By calculating the straight-line distance from her location at the end of each bout to the nutritional target, we are able to monitor fluctuations around the nutritional target in relation to behavioral decisions in actual space.

We interpret reductions in the distance from the target line as our measure of foraging success, and departures from the target line as getting further from the foraging goal. If a specific ratio of $Npe:P$ is indeed a legitimate foraging goal, and if 10.58 is not an arbitrary value in this context, then goal directed behavior in the actual environment should translate directly to

reductions in the Euclidean distance to the target ratio.

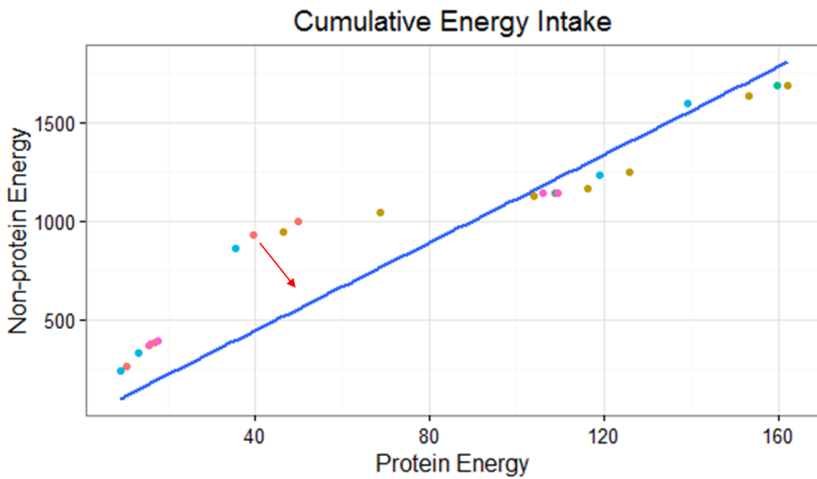


Figure 2.4 Cumulative intake of *Npe:P*: An example of one foraging day from an adult female trajectory. Each color represents a different food species, and each point represents the end of a new foraging bout. The blue line is a line with a slope of 10.58 representing the nutritional target ratio for the orangutans. The Euclidean distance from the line is our quantitative measure of foraging success.

Hypothesis 2.2

Figures 2.5 and 2.6 are linearized representations of the results of GAMMs, looking at how deviations from the nutritional rail are predicted by changes in spatial decisions by the orangutans. Table 2.5 includes results of each model. Distance from the target was strongly associated with changes in movement decisions. As individuals overshoot their target, mean persistence velocity decreases. Mean persistence is highest when individuals are closest to the nutritional rail. An increase in mean persistence velocity translates to both faster and more directed motion. Standard deviation and autocorrelation also follow the same trend. A higher standard deviation in persistence velocity means more variable starts and stops, and short bursts of speed, and a higher autocorrelation means more directed motion independent of speed.

The same trends are seen with changes in turning velocity. Standard deviation and autocorrelation in turning is highest when individuals are the closest to their target ratio of macronutrients (Figure 2.5 and 2.6). An increase in standard deviation for turning velocity

corresponds to more turns, and an increase in autocorrelation corresponds to long and wide arcs in the motion (longer turning radii). Together these results support Prediction 2.2a of Hypothesis 2.2a.

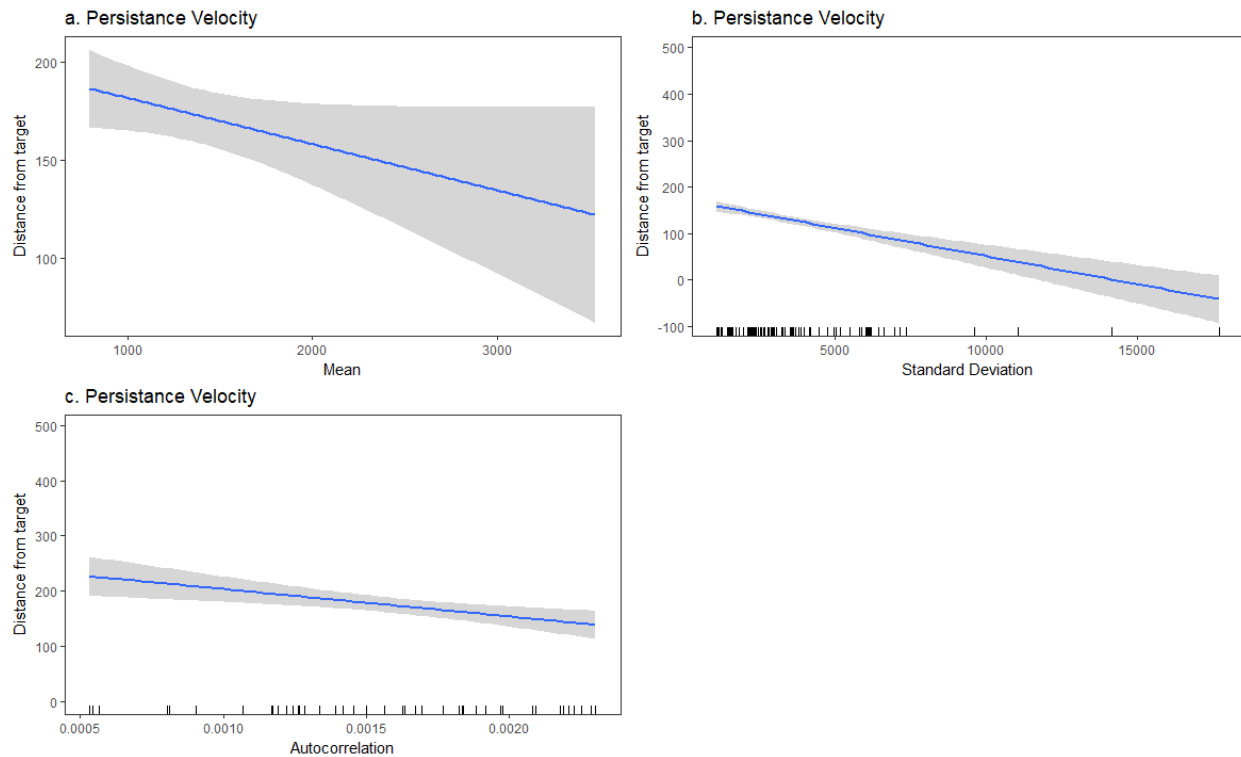


Figure 2.5 Deviations in the distance from the target rail in response to Persistence velocity: Linear representation of outputs from GAMM demonstrating how deviations from the nutritional rail are predicted by changes in mean a) mean; b) standard deviation; and c) autocorrelation in persistence velocity.

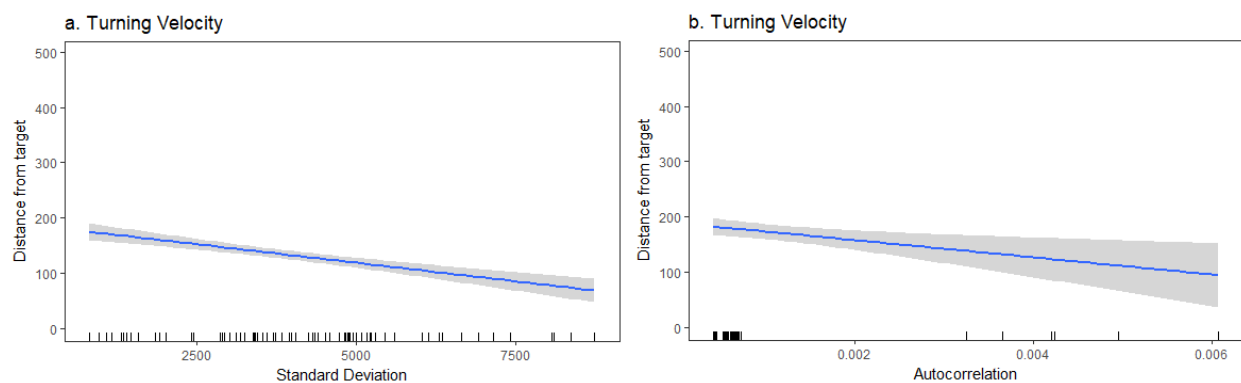


Figure 2.6 Deviations in the distance from the target rail in response to turning velocity: Linear representation of outputs from GAMM demonstrating how deviations from the nutritional rail are predicted by changes in mean a) standard deviation; and b) autocorrelation in turning velocity.

Table 2.5 Variation in distance from target ratio of Npe:P in response to movement parameters, outputs of generalized additive mixed models

GAMM	AIC	R-sq (adj)	Smooth terms	edf	Ref.df	F-value	p-value
$distance \sim \mu_{V_p} + \sigma_{V_p} + \rho_{V_p}$	8003.67	0.638	$s(\mu_{V_p})$	8.903	8.966	37.1	$< 2e^{-16}$
			$s(\sigma_{V_p})$	7.856	8.36	19.88	$< 2e^{-16}$
			$s(\rho_{V_p})$	8.93	8.998	51.85	$< 2e^{-16}$
$distance \sim \mu_{V_t} + \sigma_{V_t} + \rho_{V_t}$	8184.952	0.533	$s(\mu_{V_t})$	8.893	8.996	40.8	$< 2e^{-16}$
			$s(\sigma_{V_t})$	8.728	8.978	17.16	$< 2e^{-16}$
			$s(\rho_{V_t})$	8.975	8.999	24.4	$< 2e^{-16}$
$distance \sim \mu_{V_p} + \sigma_{V_p} + \rho_{V_p}$ $+ \mu_{V_t} + \sigma_{V_t}$ $+ \rho_{V_t}$	7552.948	0.814	$s(\mu_{V_p})$	8.667	8.877	12.925	$< 2e^{-16}$
			$s(\sigma_{V_p})$	8.023	8.54	26.704	$< 2e^{-16}$
			$s(\rho_{V_p})$	8.886	8.99	47.996	$< 2e^{-16}$
			$s(\mu_{V_t})$	8.724	8.953	18.844	$< 2e^{-16}$
			$s(\sigma_{V_t})$	7.621	8.503	8.839	$4.48e^{-12}$
			$s(\rho_{V_t})$	8.646	8.895	5.64	$1.81e^{-07}$

2.4. Discussion and Conclusion

The simulation represents an animal feeding randomly from known items in the diet. If the mean ratio of macronutrients is a biologically meaningless metric, then the observed population mean should be equivalent to the simulated values. If the target ratio of nutrients was unintentional, then it should reflect the average of the environment. In this case, observed values were significantly smaller than expected by random chance, indicating that orangutans are ingesting more protein relative to non-protein than expected. Even when high energy fruits are available, orangutans are still maintaining a higher than expected relative protein intake. These results support Prediction 2.1a of Hypothesis 2.1a.

The relationship between spatial movement and macronutrient intake is quite striking. It is clear that orangutans are modulating their spatial behavior in response to their macronutrient balance. Parameter values for both persistence and turning velocity are consistent with the

predictions for an informed search strategy. When orangutans are close to their target balance of nutrients, they exhibit faster, more directed movement, with an increase in turns and punctuated movement and longer turning radii (see Figure 2.5 and 2.6). When they are far from their nutritional target, they exhibit slower, less directed motion, with less turns and shorter turning radii. In other words, when individuals move in a random and meandering way, they start to drift further from their nutritional target, and when they move in a goal directed way, where they speed up as they move to highly valued items and make discrete turns and stops between goal items, they are able to return to their nutritional target. These results are consistent with goal directed behavior, and suggest that the orangutans are likely using non-local information, and perhaps memory, to locate the food items that enable them to achieve the observed ratio of nutrients, which is likely close to their actual needs. The movement parameters vary with the nutritional target such that they confirm our expectations laid out in Table 2.3 for informed search. The parameters do not suggest ARS when the distance to the target gets small. It could be that orangutans are exhibiting multiple modes of behavior, such that while they are engaging in non-goal-oriented behavior they start to overshoot their foraging targets. Switching to a goal directed movement mode likely enables them to correct their nutritional trajectories. The spatial movement, together with the results of the simulated nutrient ratios, indicate that orangutans make non-random foraging decisions enabling them to maintain a higher than expected protein intake.

The approach employed here may not be ideal for systems where within group competition or predation are important factors influencing movement. The orangutans at Tuanan are neither group living, nor subject to known predators, and therefore changes in their fine scale motion parameters can be more confidently interpreted. Additional data are required at sites with

group living animals or sites with a high predator density. Furthermore, these results cannot tell us the relative contributions of any particular food item to the end of day ratio of $Npe:P$. Nor can these results tell us anything about the distribution or availability of foods, or the actual travel routes used by the orangutans. What these results clearly demonstrate, is that being near the nutritional target is strongly associated with a goal directed search strategy in orangutans. The movement parameters explained a large proportion of the variation in how far orangutans are from their nutritional target. Three GAMMS were run to understand the explanatory power of the spatial movement. The first model only included the parameters for V_p , explaining 63.8% of the variation on the distance from the target. The second model only included parameters for V_t , explaining 55.3% of the variation. The third model included both V_p and V_t . As previously stated, V_p and V_t are two orthogonal components of the movement process that together should capture the totality of the underlying structure (Gurarie et al., 2009). This larger model was identified as the best model by AIC, and explained 81.4% of the variation. The movement behavior explains a remarkable amount of the nutritional trajectory of the animals. Balancing macronutrients must be considered as an important factor in the evolution of spatial decision making in animals and should be further examined in future animal movement research. While animals have been clearly demonstrated to optimize parts of their behavior for energy maximization and risk aversion, this study provides evidence that foraging behavior is also being optimized to maintain a specific balance of macronutrients in the diet.

These results support Prediction 2.2a of Hypothesis 2.2a. This provides a unique opportunity to reevaluate much of what we might predict in terms of how actual food items are ranked in the diet. Individuals overshoot their nutritional target throughout the day, regularly switching between available food items until they end on or near the target ratio. This implies

that the traditional practice of weighting food items by their assumed value (or caloric value) may be inappropriate, as orangutan food preferences may be highly temporally dynamic. Orangutans may constantly update how they prioritize food items at the end of each feeding bout, and studies modeling patch choice or predicting home-range utilization should to acknowledge that inherent underlying complexity.

Studies about spatial memory that weight goal resources by total calories may miss signals of goal directed movement. What may look like un-oriented movement may in fact be directed travel between misclassified goals. For example, Cunningham and Janson (2007) found evidence of goal directed movement and spatial memory in a wild population of white-faced saki monkeys (*Pithecia pithecia*) during a period of food abundance. They reported that the distance traveled between resources was much greater than expected at random and exceeded the estimated perceptual ranges, suggesting that the monkeys were using prior information about resource locations (Cunningham and Janson, 2007). Cunningham and Janson (2013) monitored the same group of saki monkeys during a subsequent period of fruit scarcity and failed to detect any signals of spatial memory or goal directed foraging. They attributed this change to a seasonal absence of goal resources, claiming that signals of spatial memory or goal directed behavior are only expected to manifest in the presence of goal resources (Cunningham and Janson, 2013). An alternative explanation could be that saki monkeys balance their macronutrient intake, and the misclassification of goal resources prevented the detection of goal directed foraging. The underlying structure of the saki monkey movement may indicate goal directed motion as they achieve their nutritional goals.

Distinguishing spatial memory from other forms of oriented motion in an animal that balances macronutrients still presents many challenges. As stated previously, food items vary

substantially in their macronutrient content, and animals actively balancing macronutrients are expected to recursively evaluate target food items after each feeding bout. It is possible for resources to be distributed such that many resources of differing nutritional content are found near each other. In such a case, it would be possible for an animal with the capacity for complex memory to move in a way indistinguishable from simpler forms of movement. The larger and more spread out each forging patch, the easier it could be to detect spatial memory's role in macronutrient balancing.

Given that animals make spatial decisions that facilitate macronutrient balancing, future studies may be able to predict search and navigation strategies of various taxa based on their nutritional ecology. For instance, Machovsky-Capuska et al. (2016) propose the concept of the multidimensional nutritional niche. They present a series of hypothetical models visualizing the concepts of macronutrient specialists and generalists. A macronutrient generalist tolerates a wider range of macronutrient compositions, while a macronutrient specialist will have a fixed macronutrient composition (Machovsky-Capuska et al., 2016). One might expect selection for goal direction motion to be stronger in species that are macronutrient specialists, and to utilize non-local information. One might expect macronutrient generalists to be more likely to rely on local information, or to utilize a random search strategy. The degree of specialization or generalization could have direct effects on the amount of information individuals must encode, which could have important adaptive implications. Further integration of nutritional ecology into movement ecology can greatly expand what we know about the evolution of spatial decision making.

Finally, accounting for nutritional balancing may enable us to develop better models for patch residence times and may provide a unique opportunity to revisit Charnov's (1976)

marginal value theorem. Integrating macronutrient balancing into classical optimality models is an obvious next step for future studies of nutritional ecology in wild animals. If modifying the marginal value theorem to incorporate nutrition outperforms the original model, then we can better parameterize future cognitive foraging models.

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Chapter 3. Food electivity and macronutrient balancing by Bornean orangutans (*Pongo pygmaeus wurmbii*)

3.1. Introduction

Understanding why animals select the items in their diets has been a central focus of foraging ecology research (Schoener, 1987; Perry, & Pianka, 1997; Houtman & Dill, 1998; Whelan & Brown, 2005). This stems from the optimal foraging literature, where it is suggested that animals have some understanding of food quality, rank their foods accordingly, and make economic decisions regarding what to include in their diets based on that ranking. Food quality is traditionally quantified as either calories provided or biomass, and items are ranked based on the average energy gain per search and handling time (Pyke, 1984). Food preference is typically measured in terms of use relative to availability (Altmann, 1998; Conklin-Brittain et al., 1998; Doran et al., 2002), where items that are disproportionally used relative to their availability are considered preferred food items (Lechowicz, 1982; Pyke, 1984; Lambert, 2007; Marshall and Wrangham, 2007; Marshall et al. 2009). Primatologists typically dichotomize food items into preferred or fallback foods, with fallback foods defined as both low quality and low utilization relative to their availability (Marshall and Wrangham, 2007). Marshall and Wrangham (2007) discuss the adaptive significance of these two food types, and suggest that consumption of fallback foods would select for food processing traits while consumption of preferred foods would select for food acquisition traits. A foraging animal that has some knowledge of its food resources and their traits is expected to utilize information regarding preference and quality to navigate to preferred resource locations. While Marshall and Wrangham introduce preferred foods as higher quality relative to fallback foods, they don't explore any alternative measures of food quality and how additional traits might influence food utilization.

The geometric framework literature has demonstrated that animals actively balance macronutrients to reach taxon specific, and homeostatically determined, nutritional targets (Simpson & Raubenheimer, 2012). This has been experimentally shown in many taxa, such as locusts (Raubenheimer & Simpson), caterpillars (Lee et al., 2002), bears (Erlenbach et al., 2014), mice (Solon-Beit et al., 2015), and moose (Felton et al., 2016). Nutritional balancing has also been observed in wild species, for example both gorillas and spider monkeys have been shown to switch between food items until they reach a discrete balance of non-protein energy (*NPe*) to protein (*P*) (Felton et al., 2009; Rothman et al., 2011). Humans have been shown to prioritize *P* while regulating nutrient intake (Martinez-Cordero et al., 2012). Such studies do a wonderful job exploring the net result of the balancing process. Geometric plots are used to communicate how absolute amounts of *NPe* and *P* intake vary and reveal signals of macronutrient prioritization through balancing (Simpson & Raubenheimer, 2012). Those of us studying fine-scale decision making however, are interested how macronutrient balancing unfolds mechanistically. The Geometric Framework is rarely used to predict an animal's behavior upon the sequential encounter of resources (Simpson et al. (2004) is a notable exception), and it has not been used to study the cognitive (spatial) strategies that animal use to facilitate nutritional balancing.

The geometric framework provides a convenient means of reframing our understanding of classical foraging goals. However, to study goal directed behavior, and to predict sequential foraging decisions, the relationship between food preference and nutritional targets needs to be clarified. One common means by which goal directed foraging behavior is studied is by building movement models that utilize attractiveness functions (reviewed in Janson, 2000). More recently, a popular modeling approach is to utilize recursive probability functions or redistribution kernels with explicit quality parameters (e.g. Bracis et al., 2015; Avgar et al., 2015). With any of these

approaches, the degree to which an animal is attracted to a given resource location is typically a function of distance and the value or quality of the resource. A natural next step in the utilization of these models is to use the geometric framework to determine the value parameter for each resource. This presupposes that preferred food, in terms of use relative to availability, are the items that enable individuals to reach their nutritional targets. In the geometric framework, the nutritional target is represented by a line in nutritional space with a slope equal to the ratio of macronutrients that individuals strive to attain (Simpson & Raubenheimer, 2012). It is possible that preferred foods are just as nutritionally variable as other foods, and that they are not necessarily more important than other foods in terms of reaching the nutritional target. It is necessary then, to examine how preference varies with nutrition, before assuming a nutritionally informed value metric in spatial foraging models.

One further consideration when evaluating resource quality is the rate of return of each food item. Schülke et al. (2006) studied the importance of ingestion rate for understanding energy intake. They pointed out that the amount of time spent feeding on a food item does not always equate to the relative biomass ingested. They highlighted the fact that ingestion rate varies more among food items than among individuals, and showed that ingestion rate was just as important as food chemistry in explaining variation in energy intake (Schülke et al., 2006). This poses an interesting question in terms of how to evaluate resource quality. One could simply calculate the quality of each food item as the total amount of P or NPe per gram of that food. Alternatively, the rate at which an animal is able to acquire the relevant macronutrient per unit-time of feeding may be more biologically relevant to a foraging animal. If a food is rich in some nutrient, but the amount of time required to ingest a given nutrient is high, the individual may incur a cost by choosing that food item. Thus, the overall value of this resource may not be as

high as expected based on the nutritional value alone. In this case, quality would be the rate of nutrient intake, or the interaction between ingestion rate and nutrient content. In the context of the geometric framework, this might translate to the rate at which individuals move towards or away from the nutritional rail (in nutritional cartesian space) throughout each day. While quality might be interpreted as the overall amount of P or NPe per item, it may also be interpreted as the rate at which a given food item is able to move individuals across nutrient space (the unit rate of displacement towards or away from the target nutritional rail in nutritional space). The following chapter will explore the use of two methods that can be used in concert to supplement the geometric framework while evaluating how to quantify the quality of food items.

The first method is borrowed conceptually from the seed dispersal literature. Seed dispersal landscapes (Schupp et al., 2010) are visual methods for evaluating the effectiveness of seed dispersal. They consist of bivariate plots, with one axis pertaining to some measure of dispersal quantity, and the other axis pertaining to some measure of dispersal quality. In this framework, effectiveness is the interaction between quantity and quality. Isoclines are drawn, with all values along each isocline being equal. Any points falling on the same isocline therefore share the same effectiveness value, regardless of how different their individual quantity or quality values are (Schupp et al., 2010). This makes it possible to account for the multitude of ways (or strategies) that can lead to the same effectiveness values. The use of isoclines to identify functionally equivalent values can be extended to studying the nutritive value of foods. In this case, ingestion rate is the quantity axis, and the macronutrient content is the quality axis. Each coordinate is the interaction between these two parameters, or the rate of nutrient return per unit feeding time. Items sharing an isocline exhibit identical amounts of nutrient per unit feeding time, and therefore can be interpreted as equivalent in value to the forager.

The second method, taken from classical optimal foraging literature, consists of calculating food electivity indices. Food electivity indices are a way to quantify food utilization based on use relative to availability (Lechowicz, 1982). Lechowicz compared the performance of all available electivity indices, and concluded that Vanderploeg and Scavia's (1979) E^* index (defined in section 3.2.5) is the best of the available electivity indices on the grounds that it represents the foragers perception of food value based on relative abundance. Furthermore, Vanderploeg and Scavia's E^* has a possible range of plus or minus one, making interpretation simple and convenient. Values close to one indicate preference, and values close to negative one indicate avoidance. Values at zero represent foods where use and availability are equal, and therefore likelihood of feeding is random (Vanderploeg and Scavia, 1979; Lechowicz, 1982).

Both isoclines and Vanderploeg and Scavia's E^* can be used in concert to supplement the geometric framework (GF). By utilizing the isocline values, we are acknowledging the intrinsic importance of intake rate to the value of food items and treat each item in terms of the rate of nutrient intake. We hypothesize that orangutan food preference is a function of macronutrient balancing. The combination of isoclines and E^* are utilized to make predictions. The first prediction is that if food items are different in how important they are for achieving macronutrient targets, then the nutritional profile of food items (isocline values) should be associated with E^* . If individuals prefer food items with the highest rate of return, this should translate to their ability to quickly move through nutrient space. In this case, the second prediction is that E^* should also be positively associated with the mean rate of change in Euclidean distance from the nutritional target rail per food item. In other words, food items that allow for more nutrients quickly should cause individuals to move towards or away from the target quickly, and foods that allow for faster course corrections after overshooting targets are

predicted to be preferred. Understanding the role intake rate and electivity indices play in nutritional balancing will allow us to confidently parameterize goal directed spatial models in the future.

3.2. Methods

3.2.1 Study site and system

Data were collected at the Tuanan Orangutan Research Station in Central Kalimantan, Indonesia. Tuanan is a peat swamp forest that comprises about 1137ha. Orangutan density at Tuanan is among the highest in Borneo (Husson et al., 2009), with estimates ranging from 4.3-4.5 individuals/km² (van Schaik et al., 2005; Husson et al., 2009; Vogel et al., 2017).

3.2.2 Behavioral data collection

Orangutan behavioral data were collected using standard protocols (<http://www.aim.uzh.ch/de/research/orangutannetwork/sfm.html>), and only data from full nest-to-nest focal follows were included in the analyses. For this study, nest-to-nest follows were conducted from June 2014 to August 2015. Activity and feeding data were collected using two-minute instantaneous samples. During each feeding bout, food species, food part, ripeness, intake rate, and bout duration were recorded. All data were added to the larger behavioral database consisting of data collected since 2003. All behavioral data from 2003-2015 are described in detail in Vogel et al. (2017). All analyses presented here were conducted on the pooled dataset.

3.2.3 Nutrient intake and balancing

The macronutrient compositions of each food item were taken from the long term Tuanan nutritional database consisting of 82% of the known orangutan diet. The sample collection, preparation, and nutritional analysis of each food item are detailed in Vogel et al. (2017).

P and NPe intake were calculated per feeding bout per individual per day. Cumulative intake was calculated by summing intake across bouts. The ratio of non-protein energy (kcal) to protein (kcal) ($NPe:P$) per day was calculated for all individuals from 2003-2015 using the pooled data from the long term Tuanan orangutan database. $NPe:P$ was calculated for all known individuals where nest-to-nest follows were successfully completed. The nutritional target rail for the population was calculated as the population mean $NPe:P$ (justified in chapter 2). The Euclidean distance from the target rail (d) was calculated at the end of each bout.

The rate of change in Euclidean distance per minute feeding (Δd) was calculated for each foraging bout, and the mean rate of change (Δd_{AVG}) was calculated for each food item. Δd_{AVG} is treated as the speed with which a given food item moves an individual through nutritional space. The relative position of each individual in nutritional space (i.e., P dominant space vs NPe dominant space) was calculated based on their cumulative $NPe:P$ at the end of each bout. Decision limits (Frisch, 1934) for the population mean were calculated as a way of establishing upper and lower bounds on the nutritional target. Any point where cumulative $NPe:P$ is less than the lower bound of the target rail is in P space. Any point where cumulative $NPe:P$ is greater than the upper bound of the target rail is in NPe space. The direction of movement through nutritional space is defined as equal to the ratio of $NPe:P$ of the food item being consumed. The value of $NPe:P$ of a given food item being consumed is equal to the slope of the line passing through the current location in nutrient space. Any food item with a $NPe:P$ larger

than the slope of the target rail always moves the individual towards the *NPe* portion of space.

Any food item with a *NPe:P* smaller than the slope of the target rail always moves the individual towards the *P* portion of space.

3.2.4 Nutritional intake rate and isoclines

Isocline landscapes were plotted following the example of Schupp et al. (2010). Ingestion rate forms the quantitative (y) axis, and nutritional values form the qualitative (x) axis. Isoclines are plotted like contours (Schupp et al., 2010), where points falling on the same isocline share the same rate of nutritional gain per unit time. Isocline landscapes were made for *NPe* and *P*. Nutritional gain per unit time is calculated as the interaction between ingestion rate (I_i) and either *P* or *NPe*.

3.2.5 Vanderploeg and Scavia's E^*

E^* was calculated monthly for food items from 2003 – 2015. Mean E^* was then calculated for each species across months and years. Analysis was limited to species where phenological data and abundance data were available. E^* was calculated as per Vanderploeg and

Scavia (1979), where $W_i = \frac{r_i}{\sum_i \frac{r_i}{p_i}}$, and $E_i^* = \frac{W_i - \frac{1}{n}}{W_i + \frac{1}{n}}$. r is the proportion of food i in the diet, and p is

the relative abundance in the environment (Vanderploeg and Scavia, 1979; Lechowicz, 1982).

3.2.6 Statistical analyses

Statistical analyses were done in R (R Development Core Team, 2017). Figures were generated using the ggplot2 package (Wickham, 2016). All relationships between electivity indices and nutritional values were evaluated using generalized additive mixed models (GAMM).

GAMMs were run using the MGCV package in R (Wood & Wood, 2017). They are semi-parametric extensions of generalized linear mixed models where the linear predictor involves a sum of smooth functions of the predictor variables. GAMM is advantageous because of the relaxation on parametric assumptions, making them amenable for use with E^* (Lechowicz, 1982). They are also advantageous because they can reveal non-linear relationships in the data. Individual ID and tree species ID were included as a random effect in each mixed model, and random slopes were included in the models to minimize type 1 errors. Thus, all models are fully maximal (Barr, Levy, Scheepers, & Tily, 2013).

3.3. Results

Figure 3.1 and 3.2 show isocline landscapes for P and NPe for all known food items. Figure 3.3 shows a Geometric Framework plot of all known food items. Visual inspection of the Geometric Framework plot shows that most of the diet consists of items with low total protein, with more variance in non-protein, especially for fruit. In general, plotting the entire known diet this way makes it difficult to see without excluding a large portion of items, because so many of the items are clustered in the low protein region. The isocline landscapes make it much easier to get an overview of the diet upon visual inspection, as items are much less uniformly clustered around low values. The data dispersion can be seen in Figure 3.4. Interestingly, there is much

more visual differentiation for the P landscape than for the NPe landscape. Both Figure 3.1 and 3.2 show that several items clearly fall along shared isoclines, indicating equivalence in P or NPe per minute. Means and standard deviations for each food type are available in Figures 3.1-3.3.

The difference between isocline values and raw macronutrient values is not trivial and has strong implications for how we interpret resource quality. Ranking food items by NPe results in remarkably different rankings than if food is ranked in terms of P , and ranking food items by their isocline values results in even more starkly different ranking. Table 3.1 shows the percent change in each ranking and much the average rank changed.

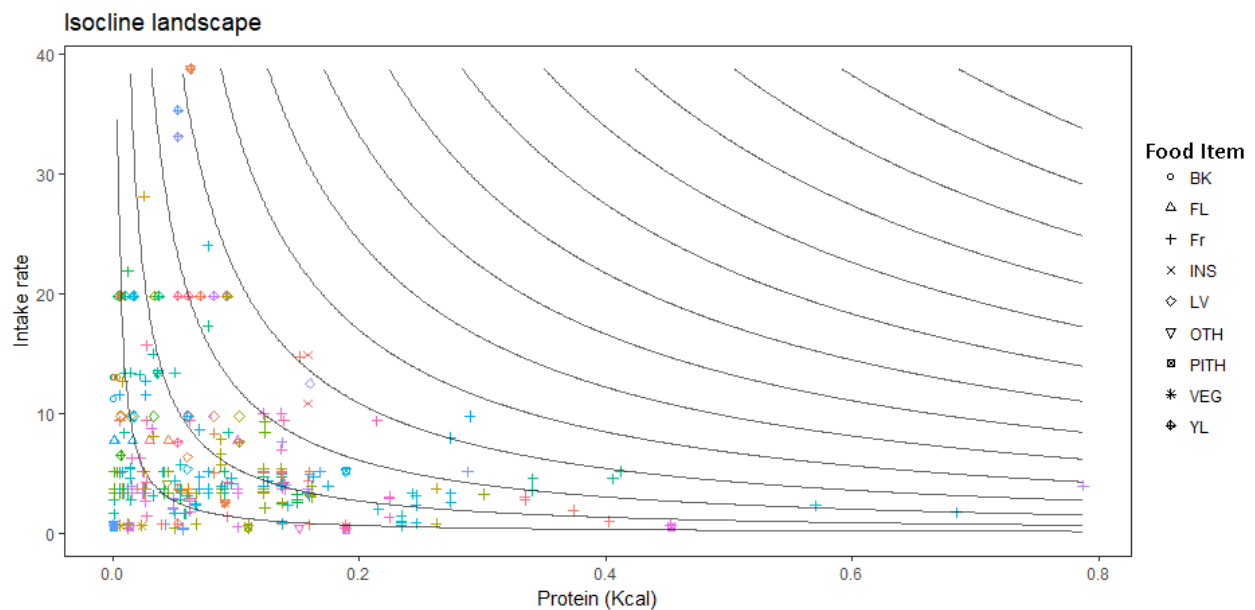


Figure 3.1 Rate of protein return per minute per food item. Colors indicate different species. Shapes indicate the food type. BK is bark, FL is flowers, FR is fruit, INS is insects, LV is leaves, PITH is pith, VEG is soft green vegetation, YL is young leaves, and OTH is other food items. All isoclines represent the interaction between intake rate and protein (Intake rate \times protein), and points along each isocline indicate equivalent values of protein per minute. The isocline landscape reveals the variety of ways each food item contributes to the rate of protein intake for orangutans. Means and standard deviations for each food type are as follows. BK ($\mu = 0.01671118$, $\sigma = 0.004636872$), FL ($\mu = 0.23163389$, $\sigma = 0.083422492$), Fr ($\mu = 0.50077248$, $\sigma = 0.421845057$), INS

($\mu = 1.83971629$, $\sigma = 0.286493616$), *LV* ($\mu = 0.55579602$, $\sigma = 0.265848504$), *OTH* ($\mu = 0.69521587$, $\sigma = 0.969508551$), *PITH* ($\mu = 0.17257171$, $\sigma = 0.299908961$), *VEG* ($\mu = 0.12212246$, $\sigma = 0.072973822$), *YL* ($\mu = 0.98694611$, $\sigma = 0.404158711$).

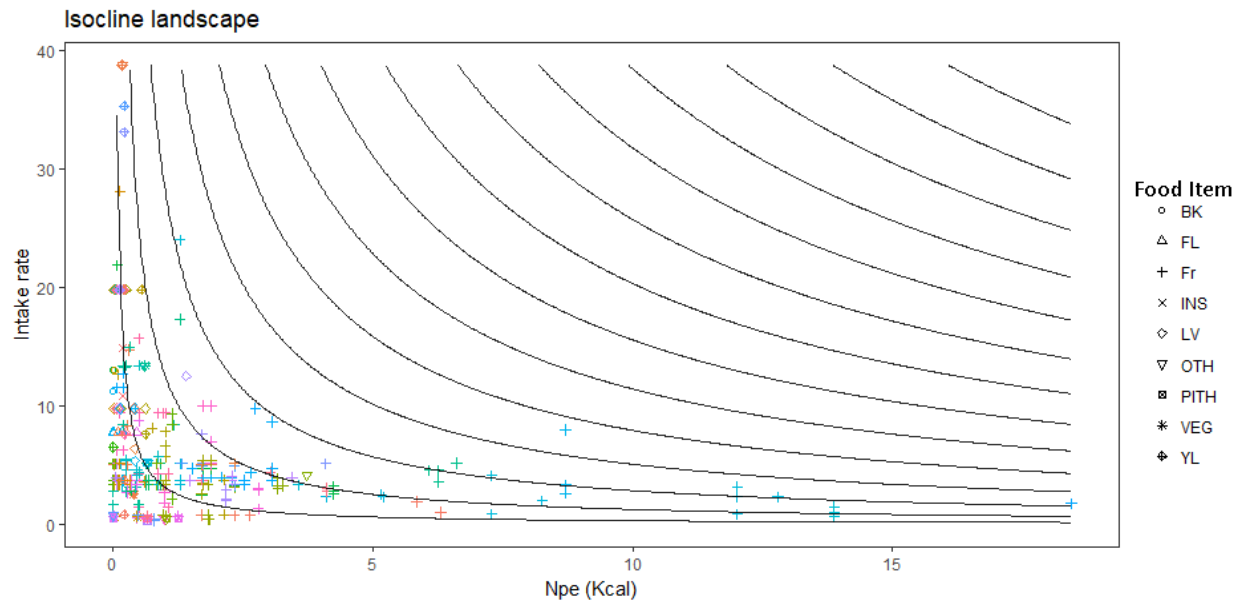


Figure 3.2 Rate of NPe return per minute per food item. Colors indicate different species. Shapes indicate the food type. All isoclines represent the interaction between intake rate and NPe (Intake rate x NPe), and points along each isocline indicate equivalent values of NPe per minute. The isocline landscape reveals the variety of ways each food item contributes to the rate of NPe intake for orangutans. Food items are the same as defined in Figure 3.1. Means and standard deviations for each food type are as follows. BK ($\mu = 0.2760019$, $\sigma = 0.0371994$), FL ($\mu = 1.9740171$, $\sigma = 0.4689325$), Fr ($\mu = 7.2566045$, $\sigma = 6.7951867$), INS ($\mu = 2.2541393$, $\sigma = 0.3510305$), LV ($\mu = 3.8033826$, $\sigma = 2.2837239$), OTH ($\mu = 4.4523942$, $\sigma = 5.1412396$), PITH ($\mu = 0.656057$, $\sigma = 1.0492328$), VEG ($\mu = 0.5769786$, $\sigma = 1.058271$), YL ($\mu = 4.1862721$, $\sigma = 1.6877476$).

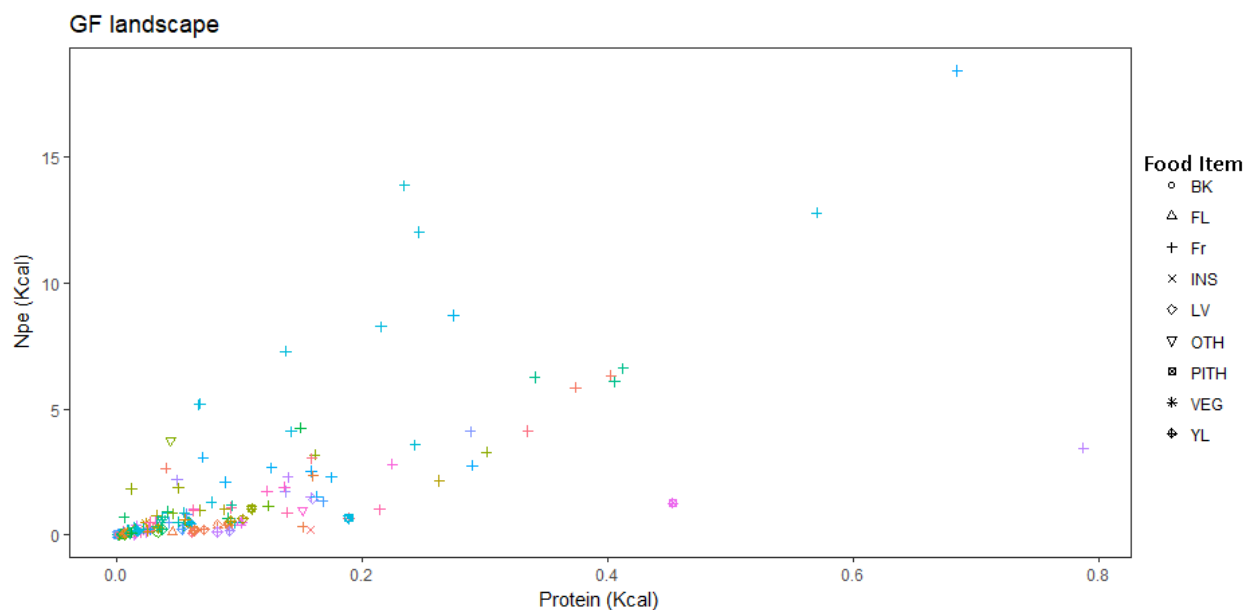


Figure 3.3 GF plot of known orangutan food items. Relative proportions of NPe to P are shown. Colors indicate different species, shapes indicate different food types. Means and standard deviations for each food type are as follows. Protein: BK ($\mu = 0.00128$,

$\sigma = 0.00035$), FL ($\mu = 0.029855$, $\sigma = 0.010752$), FR ($\mu = 0.113209$, $\sigma = 0.092931$), INS ($\mu = 0.158194$, $\sigma = 0$), LV ($\mu = 0.05878$, $\sigma = 0.022503$), OTH ($\mu = 0.085875$, $\sigma = 0.05634$), PITH ($\mu = 0.150028$, $\sigma = 0.106633$), VEG ($\mu = 0.169942$, $\sigma = 0.079941$), YL ($\mu = 0.051505$, $\sigma = 0.016297$). *Non-protein*: BK ($\mu = 0.02111741$, $\sigma = 0.002649153$), FL ($\mu = 0.25442887$, $\sigma = 0.060440188$), Fr ($\mu = 1.8886137$, $\sigma = 2.354903362$), INS ($\mu = 0.19383$, $\sigma = 0$), LV ($\mu = 0.39814574$, $\sigma = 0.185087684$), OTH ($\mu = 0.8888953$, $\sigma = 1.067834841$), PITH ($\mu = 0.61878713$, $\sigma = 0.376546151$), VEG ($\mu = 0.65126017$, $\sigma = 0.245155125$), YL ($\mu = 0.22151586$, $\sigma = 0.086016074$)

Table 3.1 Rank order changes

A	B	Percent changed	Mean position change
<i>NPe</i>	<i>P</i>	0.88	24.55
<i>P</i>	<i>P/min</i>	0.99	39.30
<i>NPe</i>	<i>NPe/min</i>	0.98	33.79
<i>NPe*</i>	<i>P*</i>	0.60	5.90
<i>P*</i>	<i>P/min*</i>	0.80	13.80
<i>NPe*</i>	<i>NPe/min*</i>	0.90	3.20

Differences between ranking systems. A is the reference ranking. Percent changed is the percentage of positions that are different from the reference ranking. Mean position change is the average magnitude of each position change.

*Rank order changes when restricted to the top ten food items.

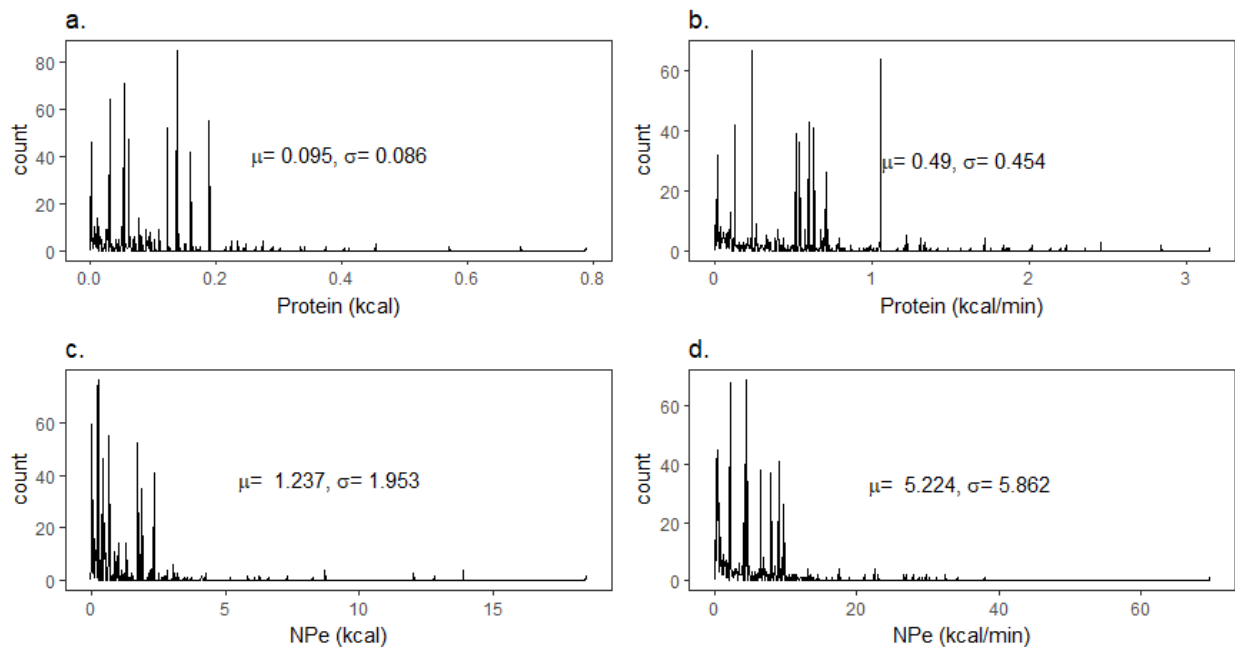


Figure 3.4 Histograms of macronutrient data. Plots a and c show the distribution and dispersion of the raw protein and non-protein values. Plots b and d show the distribution and dispersion of the isocline values indicating the rates of intake.

The variation in E^* was examined with respect to P/min and NPe/min . Both variables significantly predicted E^* , with high values of E^* associated with both high returns of P/min and NPe/min (GAMM, $p < 0.001$, $r^2=0.37$; $p < 0.001$, $r^2=0.42$). Figure 3.5 shows the GAMM

outputs. Both models show a nonlinear positive relationship, confirming prediction one.

Inspection of the rug plots indicate that the relationship is steepest where data density is highest, and credible intervals become very wide at extreme values where there are few data points.

Preference values never exceed .065 for any food item. This is likely because these are the mean preference values across years, causing seasonality to keep values from getting very high. In this case high values of E^* can be thought of as items that are consistently preferred. Once values of P/min and Npe/min get sufficiently high, the curves start to level off around the maximum values of E^* . This seems to indicate that the very high return items are equally preferred. Values of E^* for avoided items get as low as -.99, and items with E^* approaching zero are rare. This indicates that very few items are selected at random relative to their availability, and foods with low returns of both P and Npe are strongly avoided.

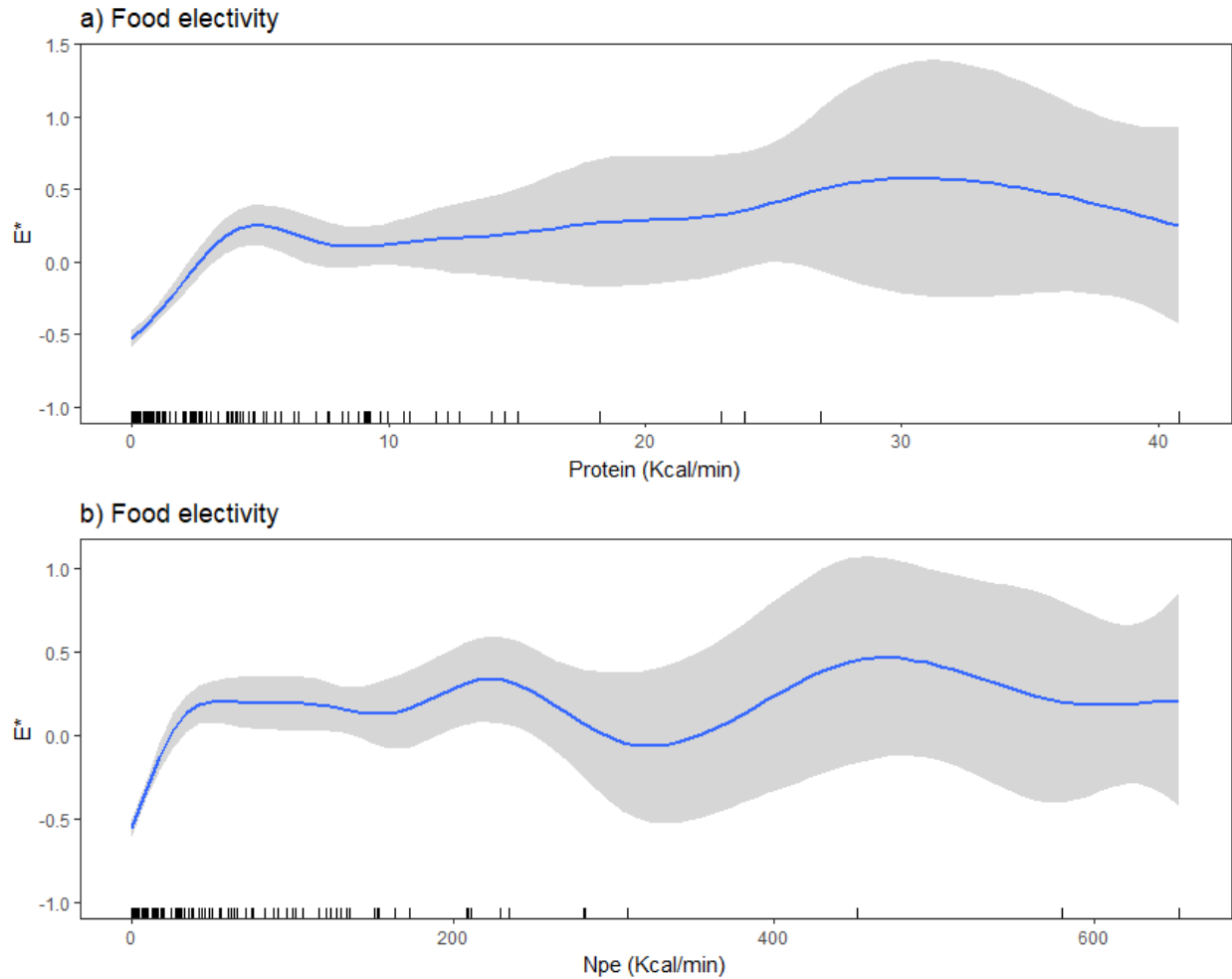
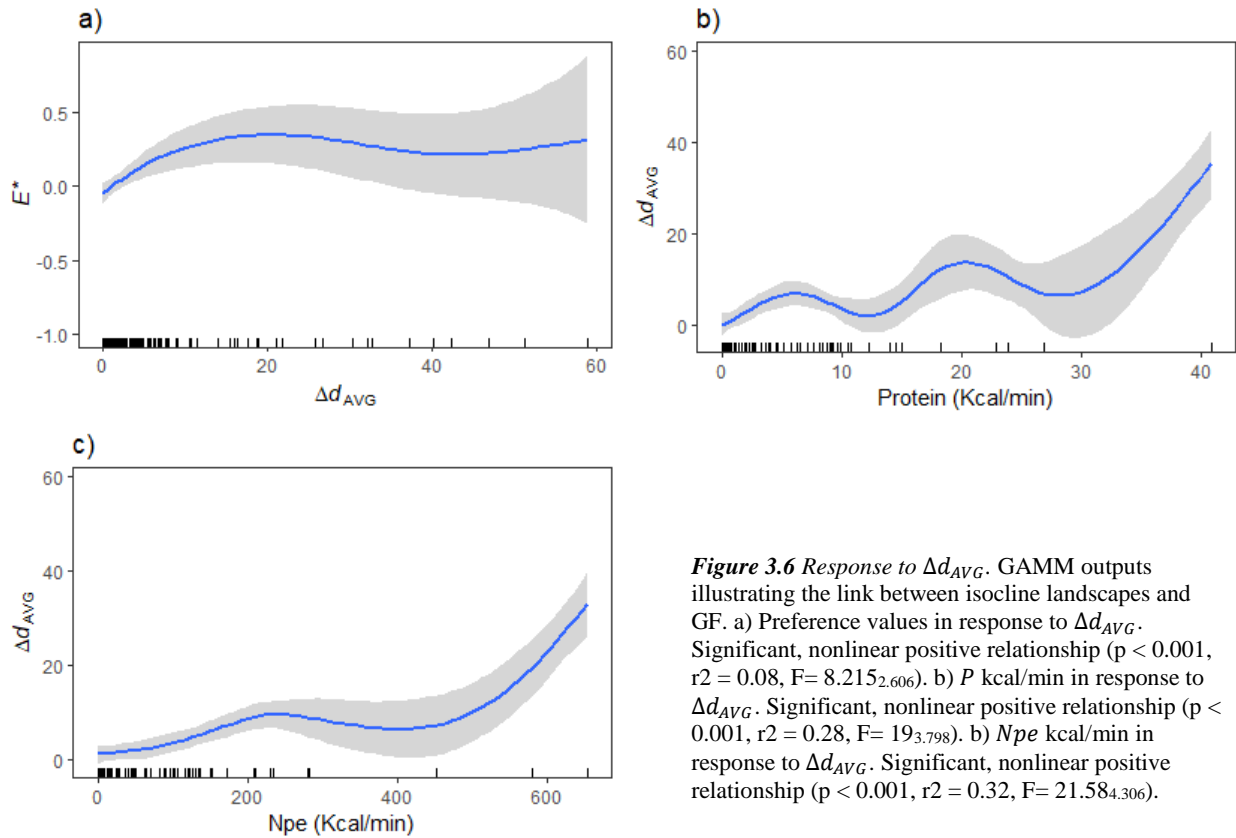


Figure 3.5 GAMM outputs of food electivity and nutrition. a) Changes in E^* in response to rate of protein return. ($p < 0.001$, $r^2=0.37$, $F = 39.63_{5.588}$). Gray bands indicate 95% credible intervals. Rug plots at the bottom indicate data density. b) Changes in E^* in response to rate of protein return. ($p < 0.001$, $r^2=0.43$, $F = 44.62_{6.919}$). Gray bands indicate 95% credible intervals. Rug plots at the bottom indicate data density.

To confirm prediction two and integrate these results back into the GF, changes in E^* , P/min , and NPe/min need to correspond to changes in an individual's trajectory through nutritional space. To accomplish this, the relationships between P/min and NPe/min with Δd_{AVG} were examined. This metric is a measure of how fast (units/min) each food item moves an individual towards or away from the target $NPe:P$. Since the rate of nutrient return significantly predicts E^* , E^* should also be predicted by the rate of motion through nutritional space. Additionally, P/min and NPe/min should be correlated to Δd_{AVG} . Individuals are predicted to

prefer food items that move them through nutritional space rapidly (have a high Δd_{AVG}).

E^* , P/min , and NPe/min were all significantly related to Δd_{AVG} (Figure 3.6). E^* , P/min , and NPe/min increased in a nonlinear positive fashion with respect to Δd_{AVG} (GAMM, $p < 0.001$, $r^2 = 0.08$; $p < 0.001$, $r^2 = 0.28$; $p < 0.001$, $r^2 = 0.32$).



Finally, for these results to be meaningful, these foraging preferences should translate to successfully attaining foraging goals. In this case, the goal of interest is the target $NPe:P$ rail as indicated by the Geometric Framework. The closer an individual gets to the target $NPe:P$ (minimal d), the greater the degree of foraging success. When individuals stray too far into P space or NPe space, the more likely individuals should choose food items that will quickly move them in the direction of the target rail. Therefore, the interaction between Δd_{AVG} , their relative position, and their relative direction in nutritional space should result in individuals reaching

their target $NPe:P$ (d should approach zero). Figure 3.7 shows the effect this three-way interaction has on d . It is clear that individuals prioritize high Δd_{AVG} foods. When individuals are in P space, they move along a rail towards NPe to return to the target rail. Conversely, when individuals are in NPe space, they moving along a rail towards P space to return to the target rail.

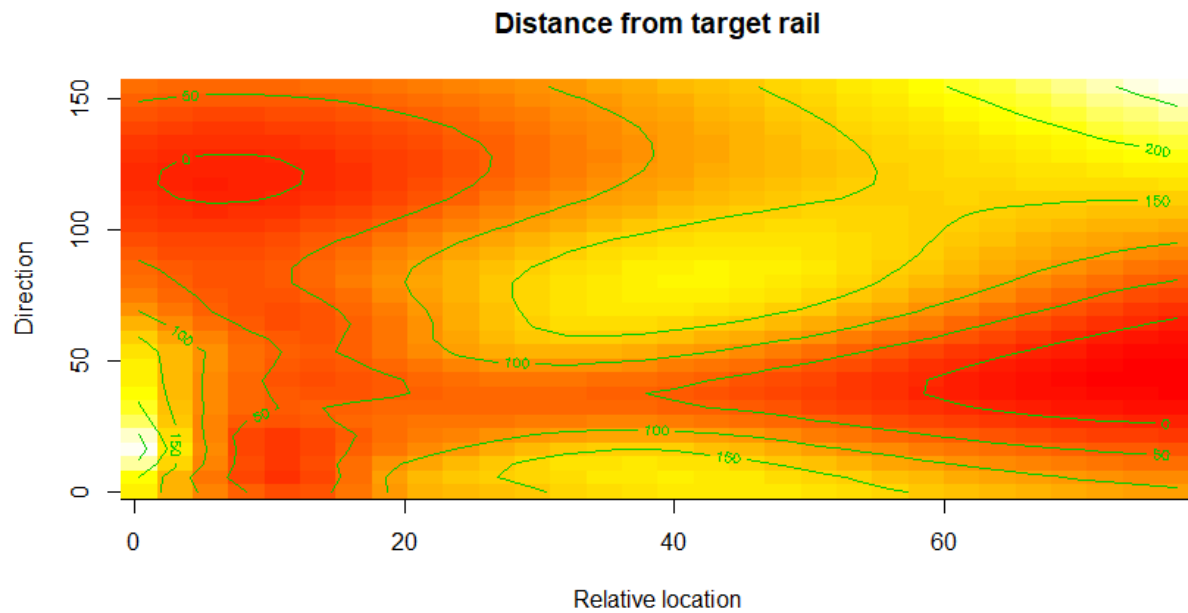


Figure 3.7 GAMM output showing how d varies in response to the interaction between Δd_{AVG} , their relative position, and their relative direction. Values are on the scale of the link function. Values to the right on the x-axis indicate animal being in P space. Values to the left of the x-axis indicate an animal being in Npe space. Values to the bottom of the y-axis indicate animals moving along a rail towards the P direction. Values to the top of the y-axis indicate animals moving along a rail towards the NPe direction. Red corresponds with small values of d at or near zero (on the $NPe:P$ target). Yellow corresponds with large values of d , indicating animals are far from the $Npe:P$ target. ($p < 0.001$, $r^2 = 0.37$, $F = 61.28_{99,86}$).

3.4. Discussion and Conclusion

These results demonstrate that orangutans are able to achieve their nutritional balance, as indicated by GF, by prioritizing food items with high rates of nutritional return as indicated by their isoclines. Food preference is related to food items that allow them to quickly traverse nutritional space, potentially to make it easier to correct their nutritional trajectory after

overshooting in any given macronutrient direction. High rate of return foods correlate with an ability to quickly change the Euclidean distance from target nutritional rails. Foods with low rates of return are heavily avoided as indicated by electivity values. Since rate of return is the interaction between intake rate and nutritional content, this means any item with an exceptionally low nutritive value and/or intake rate will be heavily avoided.

The ability to reconcile the GF outputs with actual food utilization metrics supports the notion that macronutrient balancing is a targeted enterprise, with preference for specific food items being a mechanism by which macronutrient prioritization becomes possible. The relationship between electivity values and GF outputs also assuages concerns that the nutritional balancing is largely phenomenological. The fact that fine scale foraging decisions, in terms of discrimination between food items, translates to reaching nutritional targets lends support to the notion that the GF is a useful means of quantifying resource quality and identifying foraging goals. Future resource selection modeling and step selection modeling can justifiably include food nutritional profiles as predictors of animal spatial decision making, rather than rely solely on total calories. Future studies on adaptive consequences of preferred foods in terms of cognitive evolution should consider incorporating nutrient balancing into their models, as it likely explains an important amount of variation.

It should be pointed out that isocline landscapes show promising utility for future studies of foraging behavior. Variables do not need to be limited to those included here. Any measure of quantity and quality that may have biologically meaningful interactions can be plotted using this approach. To the best of our knowledge, this study is the first to utilize isocline landscapes to analyze foraging strategies. Being able to visualize each possible way the quantity and quality axes result in functionally equivalent outcomes enables further exploration of fine scale foraging

strategies. For example, one could feasibly generate monthly isocline landscapes, and examine whether changes between quantitative and qualitative strategies enable individuals to maintain the same rate of intake. One could plot multiple individuals on a single isocline landscape and evaluate whether there is inter-individual variation in the approach to nutritional balancing. One could even use isocline landscapes in conjunction with GF to characterize qualitative and quantitative differences in home ranges between individuals based on the available food items. Isoclines and electivity indices have the potential to be very synergistic supplements to any studies utilizing the GF.

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Chapter 4. Orangutan space use and strategies for balancing nutrients.

4.1 Introduction

Movement is a fundamental characteristic of life, generated by multiple processes across a range of temporal and spatial scales. Plants are largely fixed in space yet rely on passive movement for reproduction; various forms of aquatic life rely on passive motion for dispersal and colonization; and most terrestrial forms of life exhibit active forms of motion (for further examples and discussion see Ridley, 1930; Maguire, 1963; Nathan, 2006; Guarie, 2008; Mueller and Fagan, 2008, Nathan et al., 2008; Mueller et al., 2011). Movements reflecting processes such as migration, dispersal, and colonization occur at the largest scales, instantaneous movement in response to stimuli generally occur at the smallest scales, and movement related to resource acquisition, antipredator behavior, and social behavior occur at intermediate scales (Estes et al., 1991; Alerstam et al., 2003; Gurarie et al., 2011). Furthermore, movement is directly related to individual survival, population and community structure and dynamics, and evolution (summaries and relevant citations can be found in Patterson et al., 2008; Nathan et al., 2008; Mueller et al., 2011).

The realities of conservation in the Anthropocene, along with advances in animal tracking and remote sensing capabilities, have generated further interest in animal movement research, with emphasis on the understanding of movement as it relates to invasive species, disease management, climate change, human wildlife conflict, and habitat loss (e.g. Cooke et al., 2004; Kays et al., 2007; Wikelski et al., 2007; Patterson et al., 2008; Bohrer et al., 2015; Kays et

al., 2015; Primm et al., 2015; Reynolds et al., 2015; Tucker et al., 2018). This has resulted in an associated effort to expand and improve the analytical tools and techniques for handling movement data. Sophisticated computational capabilities along with new perspectives on movement analysis have brought about a paradigm shift in movement ecology, with a move from traditional methods towards a continuous-space continuous-time modeling framework (Johnson et al., 2008; Fleming et al., 2014a; Fleming et al., 2014b; Gurarie et al., 2017).

Animal behavior is inherently continuous, with an individual's movement resulting from the complex interplay between the animal's internal state (i.e. neurological and physiological), biomechanical constraints, capacity to utilize information (cognitive or sensory), and environmental constraints (Nathan et al., 2008). Logistical constraints on the ability to sample an animal's movement require researchers to discretize the continuous movement process, sampling successive relocations (i.e. steps) along the animal's path and traditionally modeling the movement as a discrete time correlated random walk (Ovaskainen and Cornell, 2003; Bovet and Benhamou, 1988; Turchin, 1998; Bartumeus et al., 2005; Fortin et al., 2005; Codling et al., 2008). The resulting step length and turn angle distributions are used to make biological inferences about the movement process. There are a number of known problems and limitations to this approach, most notable among them being the sensitivity to sampling rate (Bovet and Benhamou, 1988; Turchin, 1996; Turchin, 1998; Bartumeus et al., 2005; Codling and Hill, 2005; Gautstead, 2013; Fleming et al., 2014a). Sampling rate is typically chosen for logistical reasons unrelated to the biology of the study system and is rarely if ever on the same time scale as the behavior of the animal. Starts and stops of behaviors are therefore unrelated to the beginning and end of sampled relocations, and the resulting distributions of steps and turns fail to capture the biological properties of continuous motion (Nouvellet et al., 2009; Fleming et al., 2014a; Fleming

et al., 2014b; Gurarie et al., 2017). Furthermore, correlated random walks are incompatible with irregularly sampled data, and most movement tracks are highly autocorrelated, violating the assumptions of most traditional analytical techniques (e.g. kernel density estimation) (Dray et al., 2010; Polansky et al., 2010; Fleming et al., 2014a; Fleming et al., 2014b; Gurarie et al., 2017).

Continuous-time stochastic process (CTSP) models are free of the above limitations. Firstly, they are defined by characteristic time and length scales that are scale invariant, and therefore independent of sampling schedules and robust to irregular sampling. (Johnson et al., 2008; McClintock et al., 2014; Fleming et al., 2014a; Fleming et al., 2014b; Gurarie et al., 2017). Secondly, rather than treating autocorrelation as a nuisance parameter, multiscale autocorrelation structures are accommodated. The CTSP modeling framework therefore provides a workflow whereby a model selection approach is applied to the autocorrelation structure of the movement process, enabling a suite of model types to be fitted to data. (Fleming et al., 2014a; Fleming et al., 2014b). Thus, the underlying movement process of an animal no longer needs to be a priori assumed, and more complicated modes of behavior across all timescales can be explored. (Fleming et al., 2014a; Fleming et al., 2014b). Previously, CTSP models were computationally inaccessible to the greater research community due to unfamiliarity with the underlying mathematics. Thankfully, there are now well documented tools enabling the widespread application of these methods to the analysis of fine-scale and large-scale space use (Fleming and Calabrese, 2015; Gurarie, 2015; Johnson, 2015; Gurarie, 2016).

Logistical and ecological considerations make orangutans particularly appropriate study candidates for a CTSP modeling approach. Currently, the risk of obstructing the throat sack precludes orangutans from being fitted with traditional GPS collars, and they are very skilled at removing affixed devices (personal experience). Tracking orangutans is therefore restricted to

sampling with hand held GPS units during focal observations. Naturally, this results in unevenly sampled tracking data that have time gaps, as animals occasionally evade researchers over the course of focal observations. Furthermore, orangutans often leave the boundaries of study areas, returning at unpredictable time intervals. This makes it nearly impossible to evenly sample orangutan space use. Because the characteristic scales of CTSP models are defined independently of the sampling rate, and because CTSP models don't assume independent and identically distributed data, the CTSP framework is well suited for analyzing orangutan movement data.

Ecologically, orangutans exhibit a suite of interesting external and internal components to their movement. They occupy multiple forest types, with a majority of individuals occurring in degrees of anthropogenically modified forests (Singleton et al., 2004; Meijaard et al., 2010; Wich et al., 2012; Ancrenaz et al., 2015). They are therefore subject to multiple canopy structures which influence their locomotion (Hebert and Bard, 2000; Thorpe and Crompton, 2006; Thorpe et al., 2007; Thorpe et al., 2009; Manduelli et al., 2011; Manduelli et al., 2012). They are also the largest living arboreal animal, further constraining them to parts of the canopy that can support their weight (Thorpe and Crompton, 2007; Thorpe et al., 2009). Furthermore, orangutan habitats exhibit complex phenological patterns resulting in highly variable and largely unpredictable food availability (Marshall et al., 2009; Marshall and Which, 2013; Marshall et al., 2014; Vogel et al., 2017). Orangutan therefore are predicted to require sophisticated spatial strategies to account for the external drivers of their motion, i.e. both locate uncertain resources and manage physical movement constraints.

Recent studies have found that during periods of fruit scarcity, orangutans metabolize body fat, indicated by ketone bodies in their urine (Knott, 1998; Thompson and Knott, 2008)

enter into a negative energy balance as indicated by low C-peptide of insulin levels (Thompson and Knott, 2008), and enter into a steady-state negative protein balance, as evidenced by $\delta^{15}\text{N}$ levels (Vogel et al., 2012a; Vogel et al., 2012b). Given these measurable responses to food scarcity, selection can be predicted to heavily favor individuals with spatial strategies that prevent chronic states of energy and/or nutrient deficits. Furthermore, selection for spatial memory is suggested to be stronger in environments where scarcity is higher and where relative abundance of food is lower (Marshall and Wrangham, 2007; Croston et al., 2015). Thus, there are also clear internal components to orangutan movement, physiological and cognitive, that likely explain not only the impetus to move, but suggest movement can be driven by non-local information, possibly through a processes such as memory and cognition.

Chapter two of this dissertation showed that orangutans intake higher proportional amounts of protein than expected by chance, and that maintaining a target ratio of macronutrients was associated with signals of goal directed foraging behavior. It could be that the spatial location of food items with preferred nutritional profiles is an important external component to orangutan spatial movement. The use of information pertaining to the location, availability, and nutritional content of these food items may be a cognitive process underlying an orangutan's ability to react to that external component to its movement, thereby satisfying the internal physiological component of its motion. Given that animals are known to actively balance macronutrients as they forage (Lee et al., 2002; Felton et al., 2009; Rothman et al., 2011; Martinez-Cordero et al., 2012; Simpson & Raubenheimer, 2012; Erlenbach et al., 2014; Solon-Beit et al., 2015; Felton et al., 2016), memory and cognition could be cognitive mechanisms facilitating macronutrient balancing.

Advances in remote sensing technologies make it possible to rapidly sample high resolution environmental data across large areas. When properly ground-truthed, these data can provide remarkably complete information about the entirety of an animal's habitat. Here, remotely sensed environmental variables and CTSP modeling were used to get a mechanistic understanding of Bornean orangutan (*Pongo pygmaeus wurmbii*) space use.

First, home range behavior will be explored. The underlying parameters of orangutan motion will be estimated and used to revisit our understanding of range residence and range overlap published previously (i.e. Singleton, 2009; van Noordwijk et al., 2012; and Buckley, 2014). GPS data collection did not begin at Tuanan until 2011 (Vogel, personal communication), and previously published orangutan ranges at the site were from data collected prior to 2011 (van Noordwijk et al., 2012). Home range estimates in this study should be markedly more reliable than prior estimates. We also take a detailed look at differences in space use between males and females. Second, movement parameters of trajectories between resources within the perceptual range and resources outside the perceptual range will be studied, and the implications for memory will be discussed. Here, orangutans are hypothesized to utilize spatial memory to make decisions, and are therefore predicted to exhibit straight, and directed motion towards resources outside of their perceptual range. Remote sensing imagery will be used to generate spatial maps of orangutan nutritional goals using machine learning techniques. The cognitive mechanisms underlying the observed space use will be explored via simulation modeling using parameters drawn from the aforementioned movement and remote sensing analysis. A model simulating a memory-based movement process is predicted to explain orangutan foraging behavior better than a model simulating a perception based movement process.

4.2 Methods

4.2.1 Study site and system

Data were collected at the Tuanan Orangutan Research Station in Central Kalimantan, Indonesia. Tuanan is a peat swamp forest that comprises about 1137ha. Orangutan density at Tuanan is among the highest in Borneo (Husson et al., 2009), with estimates ranging from 4.3-4.5 individuals/km² (van Schaik et al., 2005; Husson et al., 2009; Vogel et al., 2017).

4.2.2 Behavioral data collection

Orangutan behavioral data were collected using standard protocols (<http://www.aim.uzh.ch/de/research/orangutannetwork/sfm.html>). For this study, nest-to-nest follows were conducted from June 2014 to August 2015. Activity and feeding data were collected using two-minute instantaneous samples. During each feeding bout, food species, food part, ripeness, intake rate, and bout duration were recorded. All data were added to the larger behavioral database consisting of data collected since 2003. All behavioral data from 2003-2015 are described in detail in Vogel et al. (2017). Ranging data were collected every thirty minutes prior to this study, and every two minutes for this sampling period. The pooled dataset was used for autocorrelated kernel density estimation (AKDE; see section 4.2.7). Two-minute GPS data were used for calculating fine scale movement parameters.

4.2.3 Phenology

Monthly phenology monitoring at Tuanan began in 2003 using methods described in Vogel et al. (2008) and Harrison et al. (2010). All trees with a diameter at breast height (DBH) of greater than 10cm were monitored monthly for the presence and abundance of fruit. Phenology

plots contained 1868 trees covering 2.3 ha, encompassing the home-ranges of the most commonly monitored orangutans. Tree species were identified by skilled local botanists.

4.2.4 Nutrient intake

The macronutrient compositions of each food item were taken from the long-term Tuanan nutritional database. The database encompasses 82% of the known orangutan diet. The sample collection, preparation, and nutritional analysis of each food item are detailed in Vogel et al. (2017). Protein and non-protein kcal intake were calculated per feeding bout per individual per day following Vogel et al. (2017). Cumulative intake was calculated by summing intake across bouts. The cumulative ratio of non-protein kcal to protein kcal per day was calculated for all individuals.

4.2.5 Software

All data analyses and simulations were conducted in the R environment for statistical computing (R Core Team, 2017). Generalized additive models were run using the *mgcv* package (Wood and Wood, 2015). Random Forest was run using the *randomForest* package (Liaw and Wiener, 2002). Confusion matrices were generated using the *caret* package (Kuhn et al., 2015). Semi-variograms, periodograms, model fitting, model selection, home range estimation, and home range overlap were all implemented using the *ctmm* package (Calabrese et al., 2016). Behavioral changepoint analysis was implemented using the *BCPA* package (Gurarie, 2013). Geospatial layers were handled using the *raster* and *rgdal* packages (Hijmans and van Etten, 2014; Bivand et al., 2018). Figures were generated using base R and *ggplot2* (Wickham, 2016; R Core Team, 2017).

4.2.6 Nutritional mapping

To examine the spatial strategies of orangutans as they pertain to nutritional balancing, an effort was made to spatially contextualize their nutritional landscape. Since manually identifying and mapping the location of each individual tree within the study area was infeasible within the sampling period, rapid and large-scale sampling was achieved via remote sensing. First, a reference dataset was collected to enable ground truthing of remotely sensed data (see *Reference data collection*). Following ground sampling, high resolution multispectral WorldView-3 imagery was obtained from DigitalGlobe. (see *Multispectral imagery*). High resolution spatial and spectral imagery have been shown to have great utility in remotely identifying tree species (i.e. Clarke et al., 2005; Omar, 2010; Sridharan, 2010; Chen, 2011; Cho et al., 2011; Colgan et al., 2012; Immitzer et al., 2012; Féret and Asner, 2013; Baldeck and Asner, 2014). The field reference dataset was then used to train a machine learning algorithm to identify trees based on their spectral signature (see *Tree classification*).

Following tree identification, nutritional maps were not attempted for any months where nutritional data were not available for all tree species. Furthermore, months where liana consumption was high were also excluded, as lianas could not be detected with the available image resolution. Finally, nutritional mapping was restricted to months where only the most accurately identifiable tree species were productive (see results section). For months where all criteria were met, quality indices based on tree species nutritional profiles (see section 4.2.7) were mapped to represent the nutritional balancing landscape. These maps were then utilized in orangutan foraging simulations.

Reference data collection

50m X 50m plots were established along the length of focal orangutan travel routes. All trees with a DBH of 10cm and larger were sampled, and any tree where feeding was observed by an orangutan was sampled. A total of 10,000 trees were sampled throughout the entire study period. Height, diameter at breast height, crown diameter species, and GPS coordinates were sampled for every tree. Tree height and crown extents were recorded with Nikon Forestry PRO Laser Rangefinders. Garmin GPSmap 60CSx, GPSmap 62, and GPSmap 78, and Trimble Juno 3B handheld GPS units were used to record the locations of all trees. The coordinates of each tree were averaged until the estimated error reached 3m or less. New permanent identification numbers were attached to each newly sampled tree. Additionally, seven 50m X 50m biomass plots were established where all trees were sampled regardless of DBH. With a team of four people sampling trees and one person observing the orangutans, we found that a minimum of one plot and a maximum of two plots were possible to finish in one day.

Multispectral imagery

Available WorldView-3 images for the dates of the study period were chosen based on lack of cloud obstruction and absence of smoke from local agricultural burning. Due to local weather conditions and the prevalence of local burning, finding suitable images was challenging. Two images were deemed suitable, one from August 2014 and one from April 2015. The first image was during a dryer time of year (mean daily rainfall = 2.5mm), and the second image was during a wetter period (mean daily rainfall = 8.7mm). The WorldView-3 satellite provides high spatial resolution data at 1.38m per pixel with a geolocation accuracy predicted at less than 3.5m without ground control. Multispectral images include 8 spectral bands: Coastal (397–454 nm),

Blue (455–517 nm), Green (507–586 nm), Yellow (580–629 nm), Red (626–696 nm), Red Edge (698–749 nm), Near Infrared 1 (765–899 nm), and Near Infrared 2 (857–1039 nm). DigitalGlobe has published descriptions of the utility of each band. The Coastal and Blue bands provide measures of chlorophyll content in healthy plants. The Yellow and Green bands are measures of plant health, and when used together help differentiate types of plant materials. The Red band is one of the most important for discriminating vegetation from soil and geological features. The Red Edge band is thought to help with species and age differentiation and is also a measure of plant health. The Near Infrared 1 (NIR1) band helps measure moisture content in plants and can differentiate vegetation from bodies of water. The Near Infrared 2 (NIR2) band overlaps with NIR1, but because it is less sensitive to the atmosphere it is thought to enhance vegetation analysis (DigitalGlobe, 2013). Further specifications about the WorldView-3 system can be found on the DigitalGlobe website (<https://www.digitalglobe.com/resources/satellite-information>).

Tree classification

Remote tree identification was done using Random Forest classification (RF). RF is a non-parametric ensemble learning technique, free of the assumptions of normality or equal covariances typical of other classification methods (Breiman, 2001; Liaw, 2013). RF works by constructing a large (user defined) number of decision trees from a training dataset. Each decision tree is constructed by sampling with replacement from the training data. A random subset of the input variables is selected at each node, and the best-splitting variable is chosen based on the Gini criterion. After training, new data are classified by taking the mode of the classification outcomes of the entire forest of decision trees (Breiman, 2001; Liaw, 2013).

Measures of variable importance are given in the form of mean decrease in accuracy (MDA) and mean decrease in Gini (MDG) (Breiman, 2001; Liaw, 2013).

Here, we use a pixel-based approach for identifying trees from our multispectral images. This is because we lacked the resolution to apply automated crown delineation methods, prohibiting an object-based approach. The mean diameter of a tree crown for trees with a minimum DBH of 10 can span between ~3-4 pixels, with the largest observed crown encompassing ~10 pixels and the smallest ~1 pixel. The GPS averaged locations of our manually identified trees (our training data set; see *Reference data collection* above) were used to extract the associated pixel values from the multispectral layer. Stratified sampling of 40% of the reference dataset made up the training data for RF. The number of decision trees was set to 10000, and all 8 spectral bands were included in the model. Classification was attempted for 65 classes, 9 of which only genus level information was available at the time of ground sampling. The remaining 56 were identifiable to the species level. Model performance was evaluated by calculating the balanced accuracy from a confusion matrix (Valdez, 2007; Brodersen, 2010).

4.2.7 Movement analysis

Home ranges and periodicities

Home range analysis was restricted to individuals that were routinely followed; whose identities were known, verified, and reliably recognized by observers; and to individuals with enough full nest to nest follows whereby the total observation time added up to at least one year of observation. The final dataset included 18 individuals, with 7 flanged males and 11 adult females. Flanged male home range estimation is famously difficult. Because GPS tracking devices can't be fitted to orangutans, and because flanged males typically travel well outside the

boundaries of most study areas, continuous observation of males hasn't been successful (although there have been admirable attempts, see Buckley, 2014). Our study site is no exception to this trend. Flanged males are sporadically encountered, ranges are very large, and they typically range outside the bounds of where we are permitted to follow them. For these reasons, all male home range estimates in this study are likely underestimates due to sampling bias.

Semi-variogram and periodogram analysis were used as an initial visual exploration of movement behavior across time scales. The autocorrelation structure of the movement was revealed through visual inspection of the semi-variograms (Fleming et al., 2014a, Fleming et al., 2014b). The continuous time movement models typically studied in the context of animal tracking data include Brownian Motion (BM), Ornstein–Uhlenbeck (OU) motion, Integrated Ornstein–Uhlenbeck motion (IOU), and the newer Ornstein–Uhlenbeck–F (OUF) process. A linear increase in semi-variance at the shortest timescales indicates uncorrelated velocities characteristic of BM and OU processes, while upward curvature indicates autocorrelated velocity characteristic of IOU and OUF motion (Fleming and Calabrese, 2013; Fleming et al., 2014a). At the longest timescales, failure to reach an asymptote signals either under sampling, or that the individual hasn't established a home range. Asymptotic behavior is indicative of range residence, with the home range crossing time corresponding to the timescale at which the semi-variance asymptotes (Fleming et al., 2014a).

Periodicities in space use were explored through visual inspection of the periodograms. A periodicity in space use refers to a repeated visit to an area within the home range at a characteristic time interval (Péron et al., 2016; Péron et al., 2017). This is distinct from normal revisits to previous locations, because individuals do not necessarily occur at characteristic, predictable/cyclical time intervals. Peaks in the periodogram reveal the timescales of potential

periodicities in the mean. In other words, the animal reverts to a point in its range that moves periodically at some characteristic timescale. This is known as a periodic-mean process.

Periodicities can also be in the form of a stochastic rotational component of the movement called a circulation process, whereby individuals pass through the same areas at some cyclical time scale. A circulation process is not always visible in periodograms, and instead must be estimated directly from the data (Péron et al., 2016; Péron et al., 2017). Figure 4.1 is an illustration demonstrating periodic space use taken directly from Péron et al. (2017).

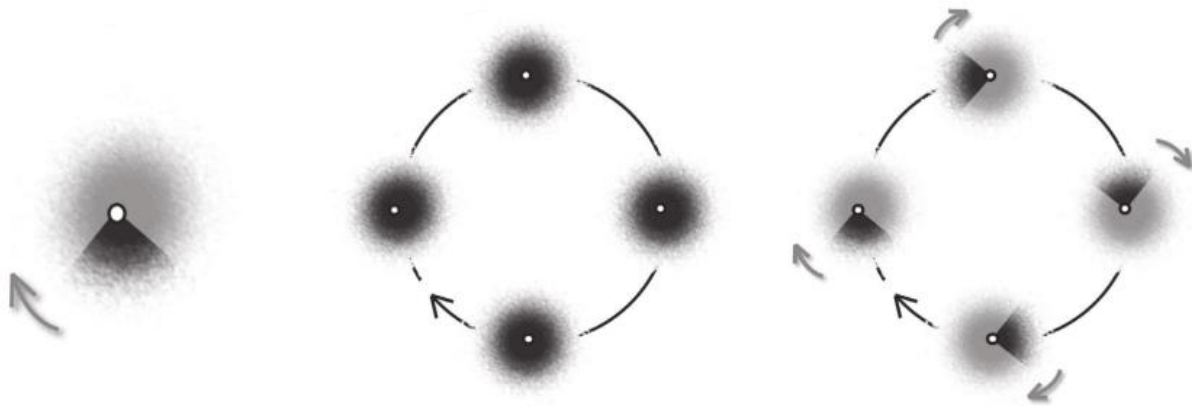


Figure 4.1 Schematic representations of periodic space use taken directly from Figure 2 in Péron et al. (2017). The left represents a circulation process, the middle represents a periodic mean process, and the right represents both. The long black arrow represents changes in the process mean while the gray arrow represents circulation (Péron et al., 2017).

Visual exploration was followed by model fitting through maximum likelihood (Fleming et al., 2014b). Candidate models were then ranked and selected according to AIC (Akaike, 1974; Yang, 2005). The selected models were compared to the semi-variograms to confirm that the important features of the data are explained (Fleming et al., 2016). The selected model for each individual was then used for autocorrelated kernel density estimation (ADKE) (Fleming et al., 2015; Fleming and Calabrese, 2017). This procedure produces estimates of home range size, position autocorrelation timescale, velocity autocorrelation timescale, and speed (km/day) (Fleming et al., 2015; Fleming and Calabrese, 2017). If a model with a periodic-mean process is

selected, then estimates of the periodic variance in position and velocity are also provided along with the number of harmonics per timescale. If a circulatory process is selected, then estimates of the length of the circulation period are provided (Péron et al., 2016; Péron et al., 2017). The position autocorrelation timescale is a measure home range crossing time. The velocity autocorrelation timescale is a measure of the tortuosity of the movement. The speed estimate translates to the average total distance traveled per day (Fleming et al., 2015; Fleming and Calabrese, 2017). The strength of the periodicities in location and velocity is the proportion of variance explained by periodicities in the mean, with the number of harmonics per timescale indicating number of periodicities at that timescale (Péron et al., 2016; Péron et al., 2017).

Home range overlap was calculated using the Bhattacharyya coefficient, a useful measure of the similarity between Gaussian distributions (Bhattacharyya, 1943). Traditionally, the Utilization Distribution Overlap Index (UDOI) has been considered the preferred method of calculating home range overlap (Fieberg and Kochanny, 2005). Recently however, it has been found that UDOI exhibits unnecessary dependence on confidence level such that the confidence level behaves like an ad hoc tuning parameter (Winner et al., in review; Fleming, personal communication). The Bhattacharyya coefficient avoids this problem completely, and is the method implemented in the *ctmm* package (Winner et al., in review; Fleming, personal communication).

Sex difference in home range behavior were analyzed using Wilcoxon rank-sum tests. The relationship between home range size and other movement metrics, and the likelihood of co-occurrence within overlapping home ranges, was analyzed using Generalized additive mixed models (GAMM). GAMMs are semi-parametric extensions of generalized linear models where the linear predictor involves a sum of smooth functions of the predictor variables. Smooth terms

are represented using penalized regression splines. Inference is based on these smooth functions (Hastie and Tibshirani, 1986, 1990; Wood, 2006a). For further information on how to calculate smooth functions, see Wood (2006b). GAMM is advantageous because of the relaxation on parametric assumptions, and because GAMM can reveal non-linear relationships in the data. Individual ID was included as a random effect in each model.

Travel distance and directed behavior

The distance traveled between food resources was calculated for all focal individuals. Behavioral Changepoint Analysis (BCPA) was used to test how signals of goal directed motion (speed and directedness) vary between trips within the orangutan perceptual range and trips beyond their perceptual range (defined in section 4.2.8). BCPA was used to calculate the tendency of motion to persist in a given direction and the velocity of that motion, captured by the “persistence velocity” $V_p = V \sin \theta$ (Gurarie et al., 2009). The mean, standard deviation, and autocorrelation of the persistence velocity were calculated at each timestep during trips between food resources (Gurarie et al., 2009). GAMM was used to analyze how these parameters vary with respect to the distance traveled to each resource.

4.2.8 Simulation

Spatially explicit, individually based models were created to explore the performance of two different cognitive strategies on nutritional balancing. The first strategy is to utilize resource information within a constrained perceptual range. In this case individuals are assumed to forage without memory and navigate towards high quality resources they can physically detect (i.e., via vision, olfaction, presence of other feeding individuals). The second strategy is to utilize memory

of resources beyond the perceptual range. In this case, how memory is encoded onto cognitive maps is not explicitly modeled. Rather, individuals are assumed to have completely explored their environment, and have complete information about resource locations within the habitat. While orangutans in the wild are unlikely to exhibit this extreme level of memory, we aim to test the importance of memory in facilitating nutritional balancing by examining which of these two extremes best recreate observed orangutan foraging behavior.

We use a modified version of the modeling approach by Bracis et al. (2015) and Bracis and Mueller (2017). Semi-variogram analysis and model selection (AIC) revealed that amongst the available continuous time movement models, the orangutan movement best fits an Ornstein–Uhlenbeck–F process (OUF) (see results section). OUF models hybridize Ornstein–Uhlenbeck motion with correlated velocity models, capturing both the restricted space use and correlated starts and stops associated with animals foraging within a home range (Fleming et al., 2014a). Orangutan movement was therefore modeled as a continuous trajectory $z(t)$, given by equations 4.1a and 4.1b.

$$\frac{d}{dt} z(t) = \frac{1}{\tau_z} (z(t) - \mu_z) + u(t) \quad (4.1a)$$

$$\frac{d}{dt} u(t) = -\frac{1}{\tau_u} (u(t)) \quad (4.1b)$$

The autocorrelation structure is captured by τ_z and τ_u , where τ_z is the timescale of autocorrelation at which an animal covers its home range and τ_u is the timescale of autocorrelation of the velocity process. To maintain a realistic autocorrelation structure, τ_z and τ_u were selected by averaging observed τ_z and τ_u values as calculated from AKDE. Values were checked to ensure the distribution of displacements approximated the observed distribution.

Unlike the original OUF model, the noise parameter is replaced by a bias vector sensu Bracis et al. (2015) and Bracis and Mueller (2017). The bias vector is described by its magnitude and angle, $u(t) = (v, \angle\theta)$. The magnitude of the bias vector, $v = \|u(t)\|$, is selected from a truncated exponential distribution with a rate parameter λ that best captures the observed distribution of orangutan displacements. The angle of the bias vector is drawn from a recursive circular probability density function (equation 4.2) (Bracis and Mueller, 2017).

$$g(\theta) = \frac{\int_0^{YR} Q(r, \theta) dr}{\int_0^{2\pi} \int_0^{YR} Q(r, \theta') dr d\theta'} \quad (4.2)$$

$r = |z - z'|$ is the distance of each point from the animal's current location z' . YR is the only parameter that changes between the memory and perception models. YR represents the perceptual range of the orangutans. We assume that orangutans rely on vision to perceive their food and that they have a similar perceptual range as humans and other primates. YR is thus set to 150m (Golla et al, 2004; Janmaat 2006). Individuals utilizing memory should be making decisions based on resources well outside their perceptual range (Janson and Byrne, 2007), thus for the memory model YR is set large enough to encompass the entire orangutan habitat. Bracis and Mueller (2017) refer to this parameterization as omniscience, and model memory as the average experience of the animal given long term time averaged remotely sensed data.

Unfortunately, a continuous record of sufficiently clear and high-resolution imaging of our site are not available. This is due both to obstruction by clouds and smoke from local burning, and the sampling schedule of available satellites. However, an examination of the performance of Bracis and Mueller's (2017) various models shows that the omniscience model most closely matches their remotely sensed memory models, as expected by a search strategy relying on non-

local prior information. It is therefore not unreasonable to interpret a model with an infinite perceptual range as functionally equivalent to the extreme case of perfect memory.

Q is the animal's evaluation of quality. In this case, quality is based on how well a given food item moves an animal towards its nutritional target in cartesian nutrient space, sensu nutritional geometry (Simpson and Raubenheimer, 2012). Figure 4.2 provides an illustration explaining this conception of Q . In a two-dimensional cartesian space where the x-axis represents protein and the y-axis represents non-protein, an animal's target balance of nutrients represents a specific trajectory through that space (Simpson and Raubenheimer, 2012). Cumulative intake of nutrients is tracked relative to the nutritional target. Here, we indicate the target as $Npe:P_T$, and the individual's current balance as $Npe:P'$. As individuals balance nutrients, they switch between food items and experience a number of overshoots and course corrections relative to the target trajectory (see chapters 2 and 3). Each food item represents a possible trajectory relative to the target. The angle of a trajectory is a function of the ratio of macronutrients (the slope) of that food item relative to the target. Here, we define a high-quality food as having a trajectory with a slope angle resulting in the greatest possible decrease in the distance from the target. In practice, this equals $\tan^{-1} \frac{Npe}{P}$ when the current ratio is too far into the Npe direction, and $180^\circ - \tan^{-1} \frac{Npe}{P}$ when $Npe:P'$ is too far in the protein direction.

$$\left(\frac{Npe'}{P} > \frac{Npe}{P_T} \rightarrow Q = \tan^{-1} \frac{Npe}{P} \right) \wedge \left(\frac{Npe'}{P} < \frac{Npe}{P_T} \rightarrow Q = 180^\circ - \tan^{-1} \frac{Npe}{P} \right) \quad (4.3)$$

At each timestep, quality is reevaluated relative to the individual's current cumulative nutrient intake, and food items are numerically ranked based on their slope angle. The probability of turning at a given angle is consequently reevaluated at each timestep using the circular probability density function.

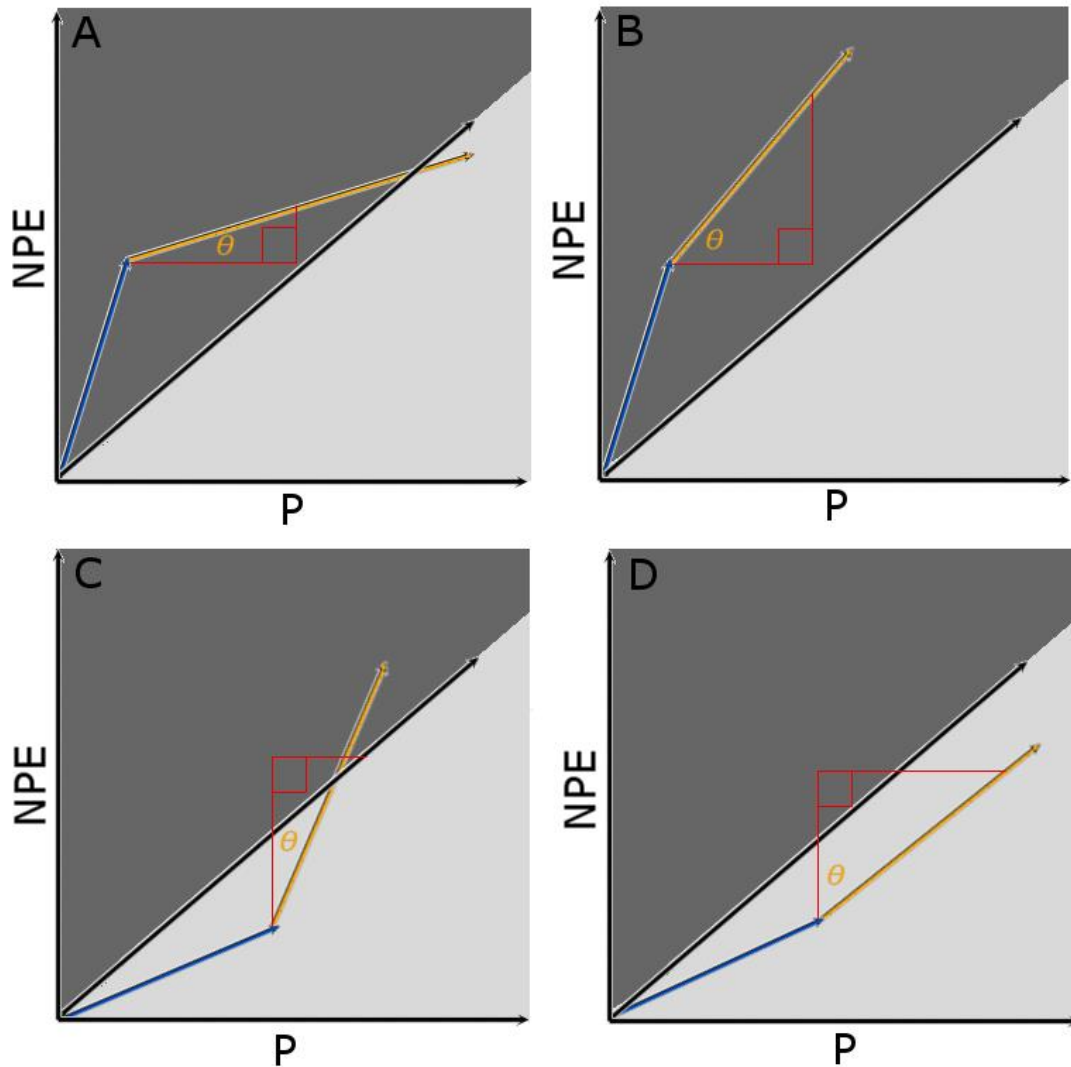


Figure 4.2 Illustration of the quality principle. The black line bisecting cartesian space is a representation of the target ratio of macronutrients. The dark gray region above the target indicates space where an individual fed on an *Npe* rich food and overshoot its target in the *Npe* direction. The light gray region below the target indicates space where an individual fed on a protein rich food and overshoot its target in the protein direction. A and B demonstrate an individual starting its foraging on a *Npe* rich food, well overshooting the target. The second bout, indicated by the orange line, shows two possible choices, food A or food B. The angle of the trajectory caused by food A enables the individual to reach its target. The angle of the trajectory caused by food B

moves the individual farther away from the target. Food A is therefore ranked as a higher quality food than food B. C and D show a similar scenario, except the individual began its foraging with a protein rich food and overshoot in the protein direction. The angle of the trajectory caused by food C enables the individual to reach its target. The angle of the trajectory caused by food D moves the individual farther away from the target. Food C is therefore ranked as a higher quality food than food D.

The simulation was run at one-minute timesteps to represent 12 hours of continuous behavior for each iteration. Models were run for 100 iterations each. The length of each feeding bout was drawn from a truncated exponential distribution with a rate parameter λ^{-1} calculated

from the observed distribution of orangutan bout lengths. The cumulative ratio of macronutrients at the end of each iteration are calculated using equations 4.4 and 4.5. P and Npe represent protein and non-protein respectively. l is bout length, I is intake rate, e is energy (in P or Npe), and b is the total number of bouts per iteration.

$$Npe:P_i = \sum_i^n \left(\frac{\sum_j^{b_i} Npe_j}{\sum_j^{b_i} P_j} \right) \quad (4.4)$$

$$\sum_j^{b_i} Npe = l_j \times e_{Npe_j} \times I_j \quad (4.5a)$$

$$\sum_j^{b_i} P = l_j \times e_{P_j} \times I_j \times P_j \quad (4.5b)$$

Simulation outputs are then compared to observed orangutan macronutrient balancing using mean squared error (MSE).

Table 4.1 contains the definitions and values of the model parameters. Both models successfully approximated the observed distribution of orangutan step lengths. MSE in step length for the perception model was 0.7, and MSE in step length for the memory model was 1.05.

Table 4.1 Model parameters and definitions			
Parameter	Definition	Units	Value
τ_z	Position autocorrelation timescale	Days	4000
τ_u	Velocity autocorrelation timescale	Minutes	4
λ^{-1}	Rate parameter of exponential distribution for generating the magnitude $ u(t) $ of bias vector v	Meters	12.32
$\Upsilon R_{p,m}$	Perceptual range	Meters	$150_{p,\infty_m^a}$
μ_z	Mean location of movement process	Meters	0

p : Perception model; m : Memory model

a Encompasses the entire study area.

4.3 Results

4.3.1 Movement analysis

Home range behavior

Semi-variograms indicated that all 18 orangutans included in the analysis are range resident.

The three parameter OUF model was strongly selected by AIC in all cases. Figure 4.3 shows the semi-variance of one individual plotted against a BM, OU, and OUF model. The semi-variance function clearly asymptotes to stable range residence. BM fails to capture the autocorrelation structure of the data, and the OU poorly fits the autocorrelation at the shortest timescales. The OUF model fits the data well across timescales. Table 4.2 shows home range size estimates and movement parameters of all individuals.

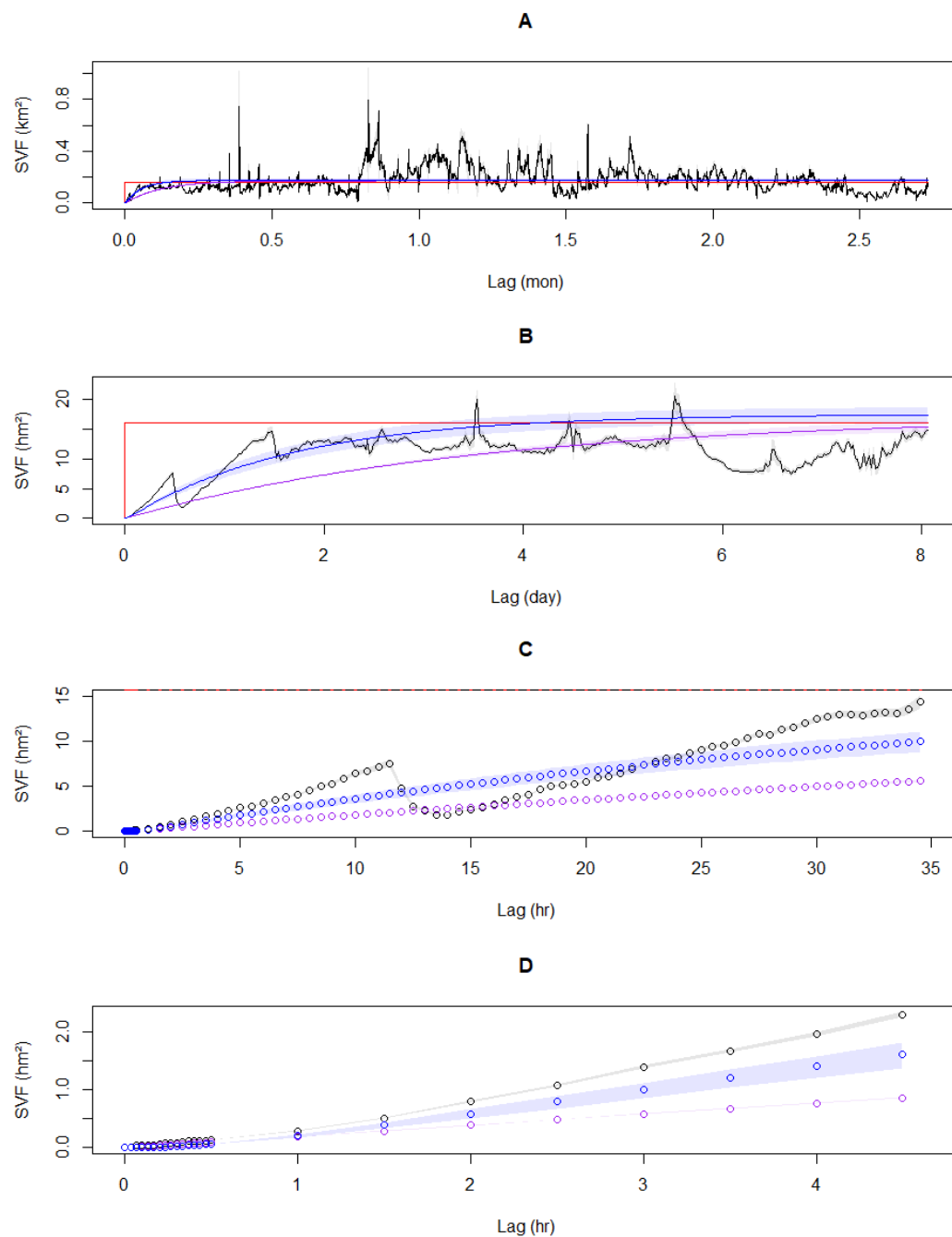


Figure 4.3 Model fits and empirical semi-variogram. Empirical variogram of a female orangutan plotted against a BM model (red), an OU model (purple), and an OUF model (blue). Plot A shows the fit across monthly timescales. Plot B is zoomed into daily timescales. Plot C is zoomed to an hourly timescale up to about a day. Plot D is zoomed further to the shortest hourly timescales.

Table 4.2 Home range estimates and movement parameters of orangutans at Tuanan. Home ranges estimated using Autocorrelated Kernal Density Estimation.

Individual	Sex	Home range (km ²) (95% CI)	Home range crossing time (Days) (95% CI)	Velocity autocorrelation time scale (minutes) (95% CI)	Average total distance traveled (km/day) (95% CI)
Milo	Female	2.79 (2.27-3.36)	1.65 (1.39-1.96)	39.80 (36.55-43.33)	2.76 (2.69-2.83)
Mindy	Female	1.99 (1.67-2.34)	1.30 (1.04-1.61)	51.32 (45.67-57.68)	2.30 (2.23-2.38)
Juni	Female	2.79 (2.30-3.35)	1.70 (1.32-2.18)	75.21 (61.36-92.19)	2.21 (2.09-2.33)
Jinak	Female	1.92 (1.46-2.46)	4.55 (3.30-6.29)	14.32 (11.58-17.70)	2.19 (2.04-2.33)
Kerri	Female	5.71 (4.18-7.48)	7.14 (5.02-10.16)	16.09 (14.15-18.29)	2.88 (2.74-2.99)
Kondor	Female	4.21 (3.26-5.29)	3.78 (2.82-5.06)	15.80 (14.34-17.40)	3.63 (3.53-3.74)
Inul	Female	1.40 (1.24-1.58)	4.04 (2.84-5.76)	14.20 (11.67-17.29)	2.45 (2.30-2.61)
Desi	Female	1.47 (1.01-2.01)	5.45 (3.98 - 7.47)	23.83 (18.86-33.11)	1.70 (1.53-1.87)
Pinky	Female	2.84 (2-3.82)	2.31 (1.60- 3.32)	39.89 (33.94-49.89)	2.87 (2.75-2.99)
Sidony*	Female	1.76 (1.14-2.5)	2.02 (0.99-4.12)	73.67 (55.72-97.41)	1.59 (1.49-1.70)
Streisel	Female	2.92 (1.65-4.55)	3.78 (1.61-8.91)	39.41 (27.38-56.73)	2.50 (2.29-2.73)
Nikko	Male	4.94 (3.87-6.15)	1.88 (1.40-2.51)	37.44 (32.43-43.22)	4.22 (4.06-4.39)
Wodon	Male	5.09 (3.80-6.56)	6.68 (4.74-9.43)	17.97 (15.17-21.29)	3.35 (3.20-3.51)
Otto	Male	6.1 (4.035-8.59)	3.87 (2.28-6.59)	40.28 (33.39-48.60)	3.04 (2.89-3.18)
Henk	Male	4.82 (2.78-7.41)	17.56 (8.84-34.89)	9.21 (7.31-11.60)	3.76 (3.59-3.93)
Helium	Male	2.55 (1.59-3.73)	3.44 (1.72-6.86)	31.48 (22.02-45.02)	2.48 (2.25-2.71)
Dayak	Male	4.52 (3.025-6.31)	5.78 (4.08-8.05)	25.59 (22.39-29.24)	3.099 (2.98-3.21)
Tomi	Male	4.35 (3.032-5.91)	3.85 (2.73-5.44)	81.90 (68.57-95.90)	1.89 (1.80-1.98)

* Deceased female (see Marzec et al. 2016).

All estimates of home range size for males are likely underestimates due to sampling bias.

Figure 4.4 shows male and female differences in home range size and movement parameters. Despite being underestimates, males have significantly larger home ranges than females (Wilcoxon signed rank, $p = 0.013$). There are no significant differences in home range crossing time (Wilcoxon signed rank, $p = 0.211$), tortuosity (Wilcoxon signed rank, $p = 1$), or average total travel distance (Wilcoxon signed rank, $p = 0.056$) between males and females.

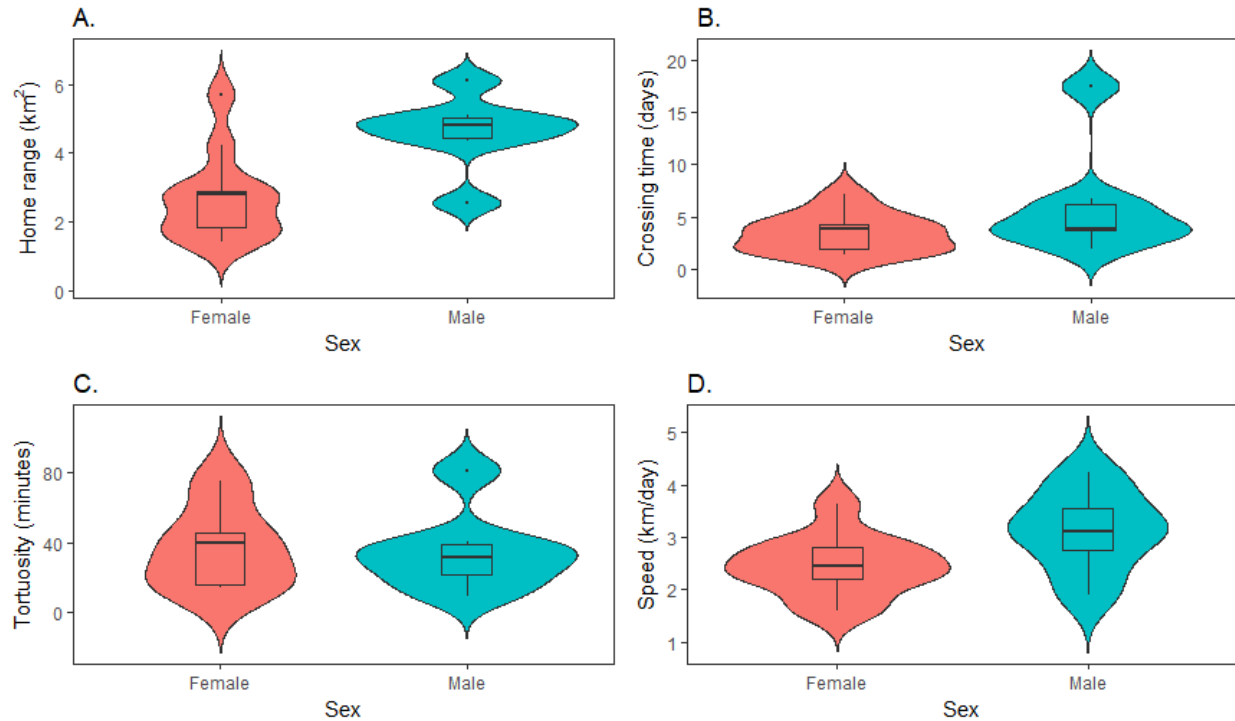


Figure 4.4 Violin plots of sex differences in A: home range size; B: home range crossing time; C: path tortuosity as measured by the velocity autocorrelation timescale; and D: average total distance traveled (speed). Each violin shows the kernelized distribution estimates with an overlaid box showing the interquartile range and a line indicating the mean. Violin plots allow for visualization of any potential multimodal distributions.

Home range size does not predict home range crossing time or path tortuosity. Home range size is positively related to average total distance traveled, with larger home ranges predicting longer total distance traveled per day (see Figure 4.5a). Home range crossing time is significantly predicted by path tortuosity, with higher velocity autocorrelation timescales (more directed movement) resulting in shorter home range crossing times (see figure 4.5b). Meandering movement with high tortuosity (low velocity autocorrelation timescales) results in longer home range crossing times (see table 4.3 for details from the GAMM outputs). Example home ranges can be seen in figure 4.6.

Table 4.3 GAMM outputs: Movement parameters

Model	F-value	r ²	p-value
Home range crossing time ~ $s(\text{Home range size})$	2.878 ₁	0.091	0.109
Average total distance traveled ~ $s(\text{Home range size})$	15.06 ₁	0.437	0.001
Tortuosity ~ $s(\text{Home range size})$	0.499 ₁	-0.032	0.490
Home range crossing time ~ $s(\text{Tortuosity})$	5.411 _{1,1.903}	0.435	0.011

Bold values indicate significant results.

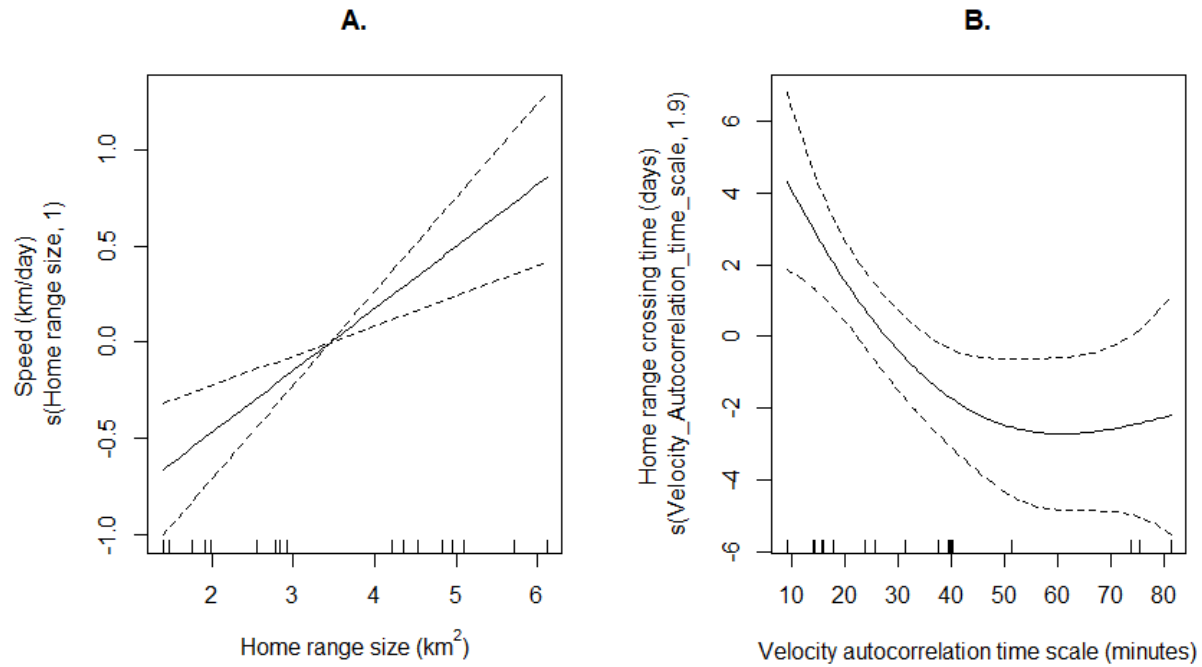


Figure 4.5 Smoothed model terms from GAMM outputs (A: Average total distance traveled ~ $s(\text{Home range size})$; B: Home range crossing time ~ $s(\text{Tortuosity})$). Model outputs available in table 4.2. Estimated effects (estimated smooth functions) are represented as solid lines, and the 95% Bayesian credible interval is represented as dashed lines. The y axis scale is in response units (on the scale of the linear predictor), and the x axis is the variable range. The y axis label is the fitted function with the estimated degrees of freedom in parenthesis, and the rug plot at the bottom indicates sampled values of the covariates of each smooth.

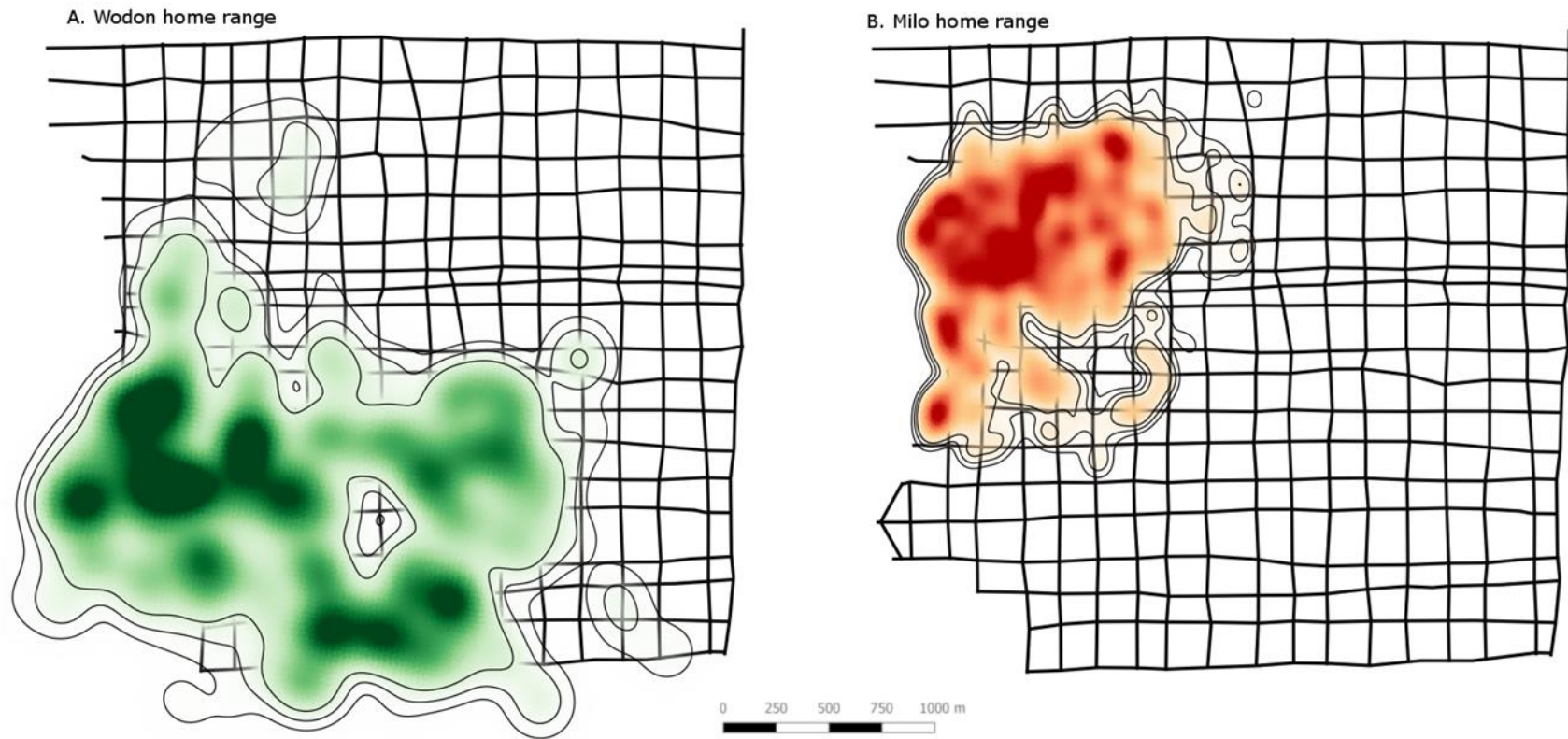


Figure 4.6 Examples of orangutan utilization distributions with 95% confidence intervals as generated through AKDE: Plot A is a flanged male home range. Plot B is an adult female home range. Dark pixels indicate the highest probability of utilization.

Periodic patterns of space use

Periodogram analysis revealed support for daily or monthly periodicities in several orangutans. Figure 4.7 shows an example periodogram from a focal female. Table 4.4 contains details about the periodicities for each individual. AIC selected models with a periodic mean process (cyclical shift in average location within the home-range) for six out of seven males, and for two females. Both females and two of the males exhibited daily periodicities, three males exhibited monthly periodicities, and one male experienced both daily and monthly periodicities. One male, and the remaining nine females were fit to a stationary mean process indicating no change in mean location within the home-range..

A circulation process was detected for five females and four males (one of the males being the one with the stationary mean process). No females exhibited both a circulation process and a periodic mean process. Four females had neither a periodic mean process nor a circulation process. All males exhibited at least one type of periodicity. The circulation frequency was similar for all individuals. The mean circulation frequency was 1.56 months with a standard deviation of 0.35.

Table 4.4 Periodicities in male and female orangutan space use

Individual	Sex	Circulation frequency (months) (95% CI)	Harmonic		Intensity of periodicity (location) (95% CI)	Intensity of periodicity (velocity) (95% CI)
			Day	Month		
Milo	Female	1.49 (0.83-7.52)	0	0	NA	NA
Mindy	Female	NA	0	0	NA	NA
Juni	Female	NA	0	0	NA	NA
Jinak	Female	1.46 (0.89-3.92)	0	0	NA	NA
Kerri	Female	NA	0	0	NA	NA
Kondor	Female	1.29 (0.77-3.82)	0	0	NA	NA
Inul	Female	NA	1	0	3.17 (0-4.84)	3.98 (0-6.03)
Desi	Female	1.79 (1.05- 6.15)	0	0	NA	NA
Pinky	Female	1.02 (0.59-3.81)	0	0	NA	NA
Sidony*	Female	NA	0	0	NA	NA
Streisel	Female	NA	2	0	6.46 (0-10.01)	15.20 (0-22.13)

Nikko	Male	NA	1	0	6.10 (0-8.84)	8.45 (0-12.18)
Wodon	Male	NA	1	0	3.37 (0.48-23.52)	6.11 (1.47-25.39)
Otto	Male	NA	0	1	42.74 (5.61-100)	3.31 (0-4.84)
Henk	Male	1.51 (0.91-6.29)	1	4	59.23 (48-73.07)	67.31 (64.16-70.61)
Helium	Male	1.44 (0.74-28.75)	0	1	19.25 (0-37.1)	1.14 (0-2.22)
Dayak	Male	1.73 (0.96-9.24)	0	0	NA	NA
Tomi	Male	2.35 (1.33-10.54)	0	1	16.52 (0-29.03)	1.66 (0-2.93)

Circulation frequency values of NA indicate that models with a circulation process were rejected by AIC. Intensity of periodicity values of NA indicate that models with a periodic mean process were rejected by AIC, and a stationary mean model was selected. The intensity of the periodicity is the proportion of the variance in the animal's location or velocity as a result of the periodicity. The circulation frequency is the average time interval the animal successively passes through (revisits) the same areas (Fleming and Calabrese, 2015). Individuals with neither a circulation process or a periodic mean exhibit no evidence of periodic space use. * Deceased female (see Marzec et al. 2016).

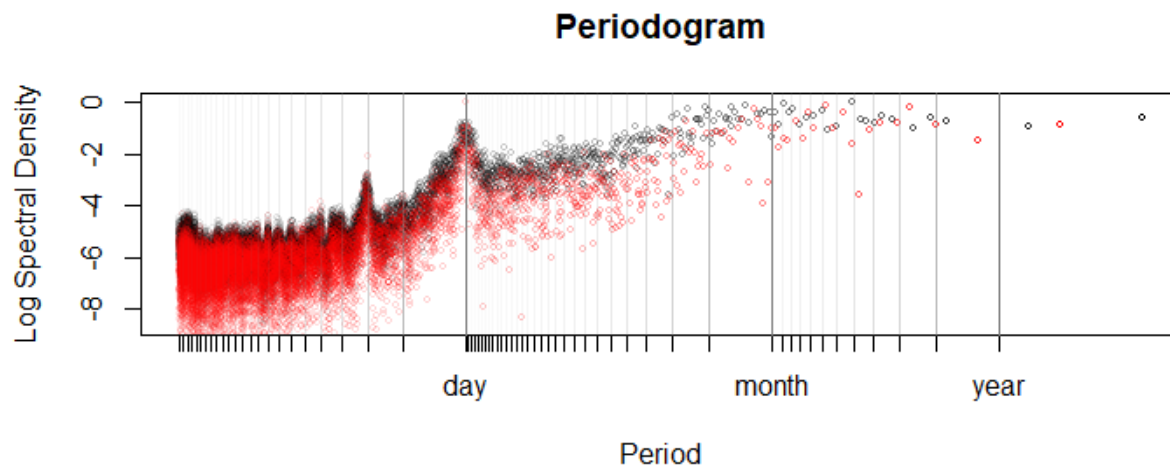


Figure 4.7 Periodogram from a male orangutan indicating evidence for periodicities at one day. Peaks are indicative of periodicities. The black represents the periodogram of the movement, and the red represent the periodogram of the sampling schedule. When they closely reflect one another, it may indicate periodicities in sampling rather than movement, requiring actual model selection to determine the likelihood of the periodicities (Fleming and Calabrese, 2015; Péron et al., 2016; Péron et al., 2017).

Table 4.5 GAMM outputs: Periodicities

Model	Smooth terms			
	Df	F-value	r ²	p-value
Presence of periodicity ~ s(Home range size)	1	3.688	0.127	0.073
Intensity of periodicity in location ~ s(Home range size)	1	1.975	0.0901	0.209
Intensity of periodicity in velocity ~ s(Home range size)	1	0.262	-0.125	0.627
Presence of periodicity ~ sex	Parametric terms			
	Estimate	t-value	r ²	p-value
	0.81818	5.292	0.614	p < 0.001

Bold values indicate significant results.

GAMM confirmed a strong relationship between sex and presence of periodicities. Males are much more likely to exhibit a periodic mean process than females, suggesting that males move between areas within their home-ranges in a predictable and temporally cyclical manner, while females generally lack this temporal patterning to their range use. There was no relationship between home range size and the strength or likelihood of periodicities. Table 4.5 provides a breakdown of model results.

Home range overlap

Mean home range overlap for orangutans was 52%. Mean home range overlap for males was 75%, and mean overlap for females was 40%. Mean overlap between males and females was 54%. Related females, specifically mother daughter dyads, exhibited substantial overlap (mean = 77%), while unrelated females exhibited very little overlap (mean = 27%). Despite the high degree of overlap, mothers and daughters still partition their space use. Areas with the highest probability of occurrence for daughters are negatively predicted by areas with a high probability of use by mothers (Figure 4.8).

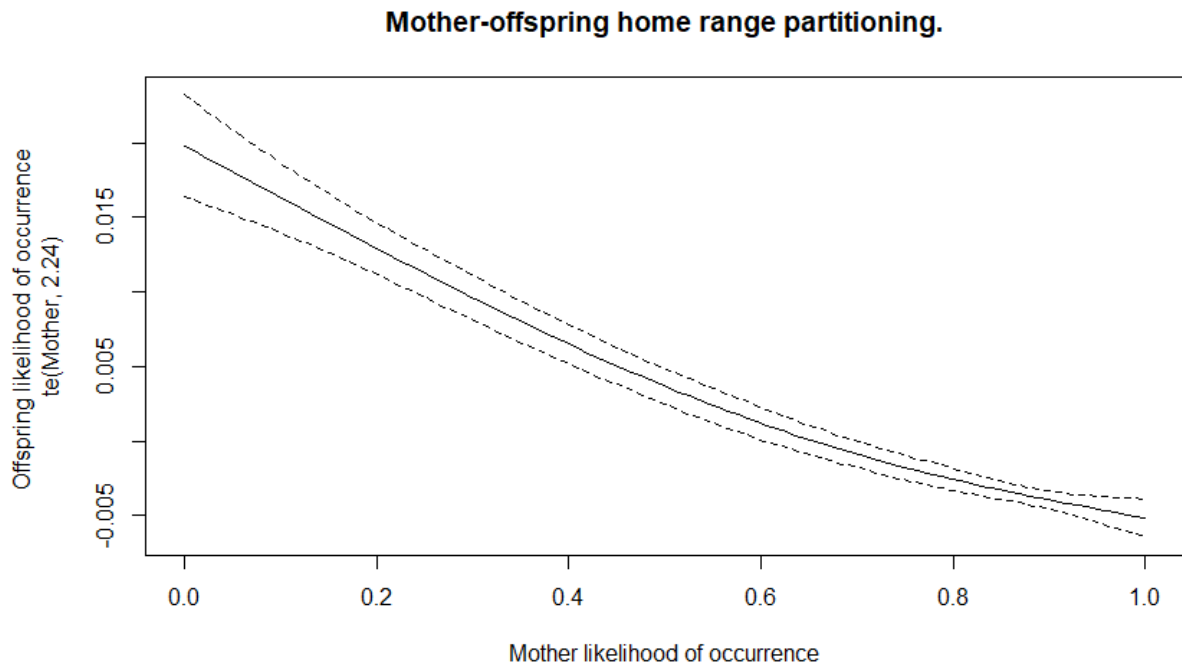


Figure 4.8 Mother daughter dyad home range partitioning. Output of a spatially explicit GAMM. Data represent the probability of utilizing a given location within the home range. Dyad identity is a random effect in the model ($F=87.75$ $_{2.722}$, $p < 0.001$, $r^2 = 0.341$). Estimated effects (estimated smooth functions) are represented as solid lines, and the 95% Bayesian credible interval is represented as dashed lines. The y-axis scale is in response units (on the scale of the linear predictor), and the x-axis is the variable range. The y axis label is the fitted function with the estimated degrees of freedom in parenthesis.

Travel to food resources

The mean distance traveled between resources was 34.5 meters. The observed length of trips to food resources best fit a gamma distribution with a shape parameter of 1 and a rate parameter of 0.81. BCPA measured movement parameters (μ , σ , and ρ of the persistence velocity) were compared for trips less than 150m to trips exceeding 150m. Neither mean velocity (μ) nor punctuations in the motion (σ) were predicted by distance traveled (GAMM, $p > 0.05$). The autocorrelation (ρ) of the persistence velocity (directedness of the motion) was significantly predicted by distance traveled. Figure 4.9 shows the results of GAMM. The nonlinear relationship between ρ and distance traveled is very informative. For all distances shorter than 150, the smooth function stays flat, with ρ not responding to distance. After 150m, there is a

sudden upward shift indicating a positive relationship between ρ and distance at the longest distances. Even though data is sparse at the longest distances, the credible intervals do not increase dramatically. This suggests that when individuals move towards resources outside of their perceptual range, they do so in a persistent and directed manner.

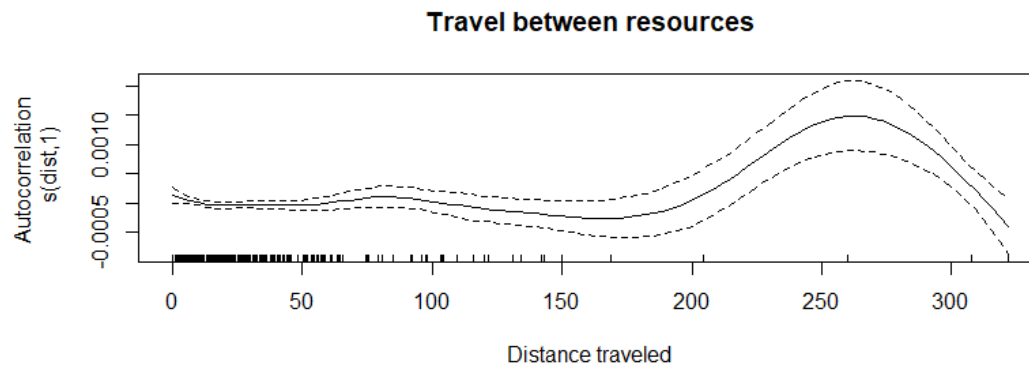


Figure 4.9 Smoothed model terms from GAMM output. F-value = 2.97_{6,917}, $p = 0.00478$, $r^2 = .056$. Estimated effects (estimated smooth functions) are represented as solid lines, and the 95% Bayesian credible interval is represented as dashed lines. The y axis scale is in response unites (on the scale of the linear predictor), and the x axis is the variable range. The y axis label is the fitted function with the estimated degrees of freedom in parenthesis, and the rug plot at the bottom indicates sampled values of the covariates of each smooth.

4.3.2 Tree classification and nutrient mapping

Tree classification by RF started with 111 tree species. After initial model training some were regrouped to the genus level, either because botanical knowledge of the species was only available at genus level, or because pooling improved model performance. This reduced the dataset from 111 to 64 classes. Figure 4.10 shows the importance of each spectral band to successful tree classification. NIR1, NIR2, and RedEdge were the most important for node splitting, while Yellow, Blue, and NIR1 were the most important for prediction accuracy. The Coastal band was consistently the least important of the spectral bands.

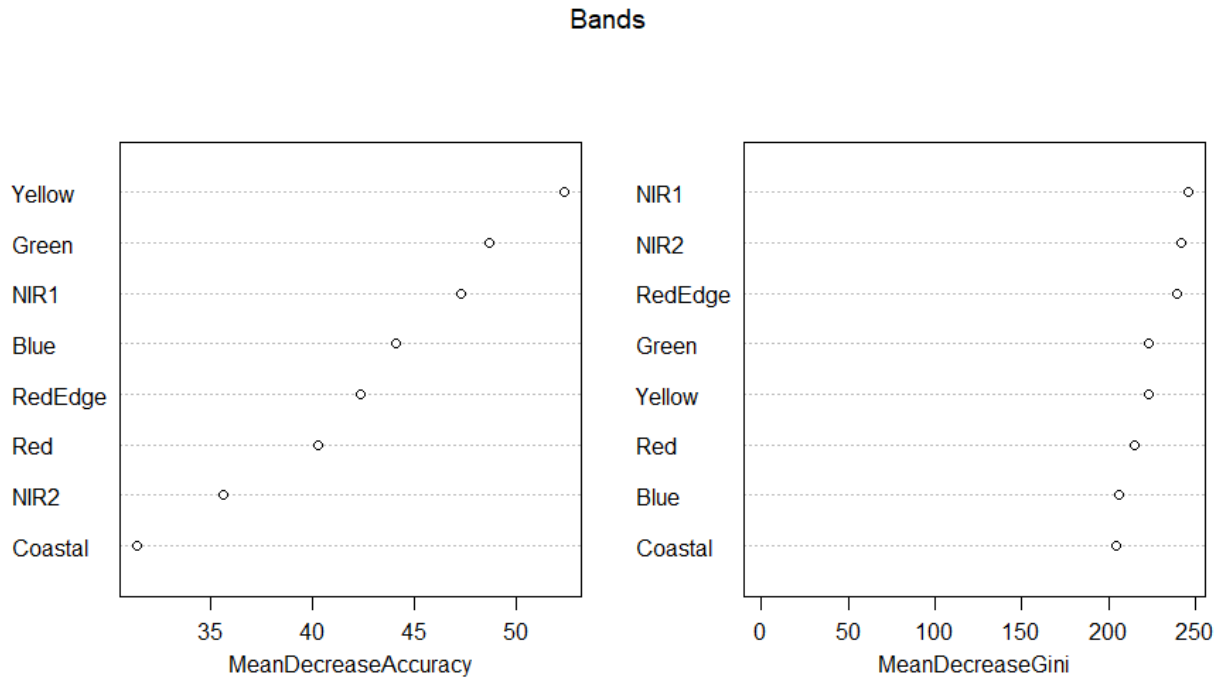


Figure 4.10 (a) Mean decrease in accuracy indicates the loss of prediction accuracy due to excluding or permuting a variable. (b) Mean decrease in Gini indicates how each variable contributes to the homogeneity of the nodes after each split during tree construction. Variables with the highest mean decrease in accuracy are generally the most important.

Balanced accuracy was calculated for each class to evaluate classification performance (details regarding the calculation of balanced accuracy are found in Kuhn, 2018). Table 4.6 provides the prediction accuracy for each class. Accuracy ranged from 70-83%, with the mean balanced accuracy for all classes being 75%. May 2015 was the only month that met all criterion for nutrient mapping (see section 4.2f Nutritional mapping). Pixels corresponding to productive species during May were classified according to RF, enabling recursive calculation of Q (see section 4.2h Simulation). **Figure 4.11** is one example of a nutrient landscape generated using RF.

Table 4.6 Random forest prediction accuracy

Species	Balanced Accuracy
Acronychia pedunculata	0.75
Aglaia rubiginosa	0.75
Alseodaphne sp.	0.75
Artocarpus dadak	0.79

Blumeodendron kurzii	0.74
Buchanania sp.	0.70
Burseraceae Santiria sp.	0.79
Callophyllum hosei	0.77
Calophyllum nodusum	0.72
Campnosperma coriaceum	0.75
Cotylelobium melanoxylon	0.75
Cratoxylum glaucum	0.75
Cryptocarya sp 2	0.72
Cryptocarya sp. 1	0.77
Ctenolophon parvifolius	0.75
Diospyros confertiflora	0.73
Diospyros pseudo-malabarica	0.75
Diospyros siamang	0.75
Dyera lowii	0.73
Elaeocarpus mastersii	0.74
Garcinia bancana	0.74
Garcinia cf. beccarii	0.73
Garcinia cf. parvifolia & sp.	0.72
Gymnacranthera farquhariana	0.79
Horsfieldia crassifolia	0.75
Ilex cymosa	0.75
Koompassia malaccensis	0.73
Licania splendens	0.70
Lithocarpus conocarpa	0.76
Litsea cf. rufo-fusca	0.74
Madhuca motleyana	0.76
Mesua sp	0.75
Mezzettia leptopoda / parviflora	0.83
Mezzettia umbellata	0.79
Mezzettia cf. leptopoda/parviflora	0.73
Mezzettia umbellata	0.75
Musaendopsis beccariana	0.75
Myristica lowiana	0.75
Neoscortechinia kingii	0.76
Neoscortechinia sp.	0.73
Nephelium sp.	0.74
Palaquium cochleariifolium	0.73
Palaquium leiocarpum	0.75
Palaquium pseudorostratum	0.75
Palaquium ridleyi	0.73
Parartocarpus venenosa	0.75

Payena leerii	0.74
Platea sp.	0.75
Polyalthia hypoleuca	0.75
Pouteria cf. malaccensis	0.76
Santiria laevigata	0.73
Shorea sp.	0.72
Stemonurus scorpioides	0.74
Sterculia sp.	0.76
Syzygium cf. garcinifolia	0.75
Syzygium cf. tawahense	0.70
Syzygium curtisii	0.72
Syzygium havilandii	0.72
Syzygium sp.	0.73
Tetramerista glabra	0.75
Tristariopsis whiliana	0.75
Xerospermum noronhianum	0.75
Xylopiia cf. malayana	0.73
Xylopiia fusca	0.79

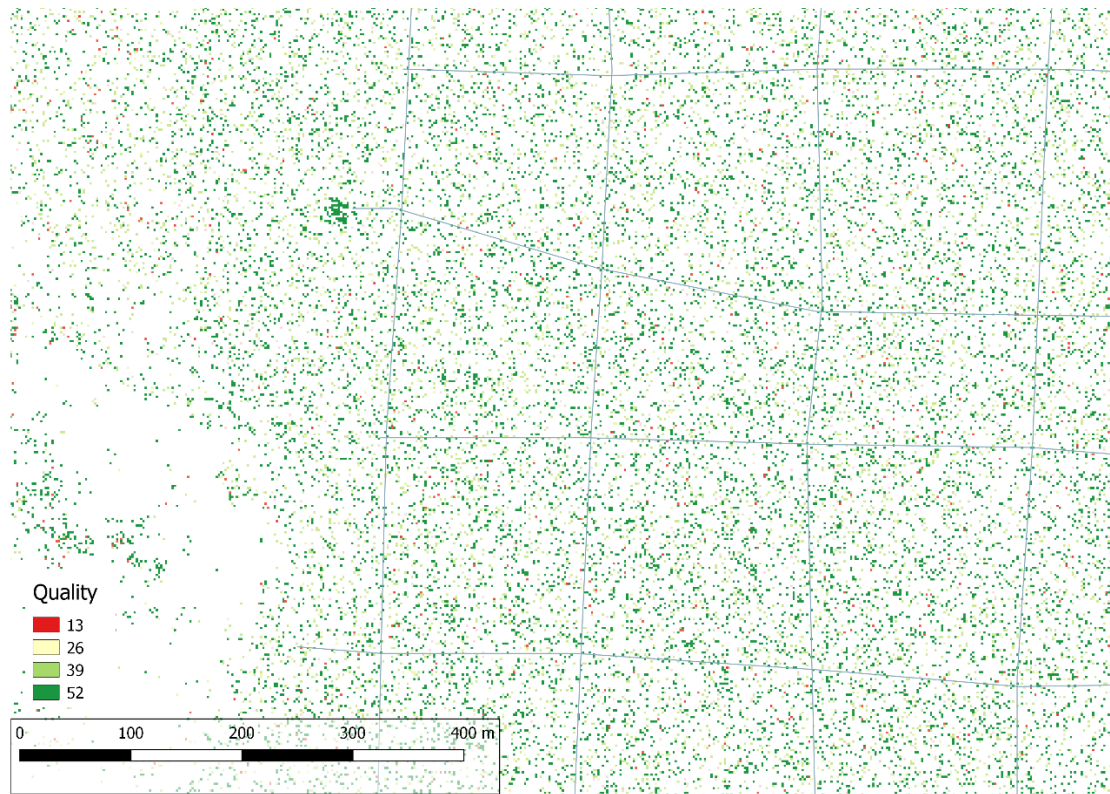
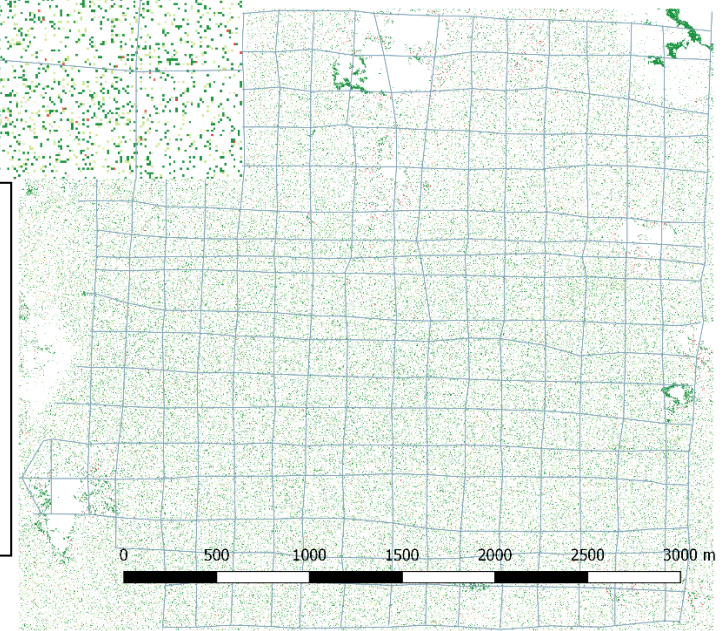


Figure 4.10 Nutritional landscape as generated using random forest. The bottom right is a site wide view of the landscape, and the top left is a zoomed in view to facilitate visual differentiation of pixel colors. Red pixels indicate nutritional profiles likely to be avoided. Dark green indicates the most attractive nutritional profiles. Pixel values are recalculated as the cumulative nutrient intake of simulated individuals changes over time.



4.3.3 Simulation results

The memory model resulted in a higher proportional intake of protein relative to the perception model. The resulting mean $Npe:P$ from the perception model was 14.35, while the mean $Npe:P$ for the memory model was 13.42. Observed mean $Npe:P$ for the orangutans in May 2015 was 13.11. The perception model overestimated Npe intake relative to the observed orangutan intake. MSE for the perception model was 4.53, while MSE for the memory model was 0.16. The results from the memory model are unexpectedly consistent with the observed values. The memory clearly outperforms the perception model, suggesting that memory may facilitate protein acquisition by orangutans. Figure 4.12 shows examples of the simulated trajectories from each model.

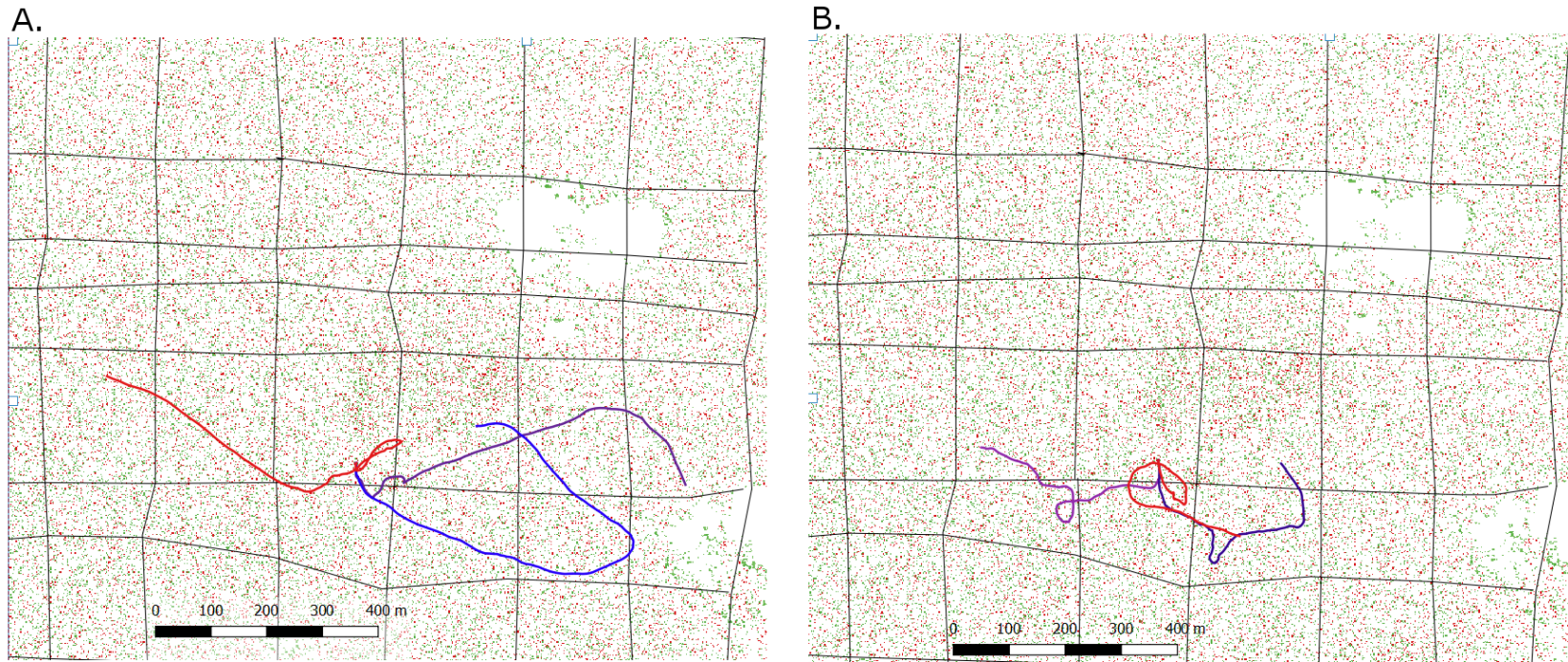


Figure 4.12 Sample simulated trajectories from the memory and perception models. *A* shows three simulated tracks from the memory model. *B* shows three simulated tracks from the perception model. Different colors indicate different tracks. Each point had a randomly selected starting coordinate. Tracks with similar starting locations were chosen for visualization purposes. Each track represents one 12-hour day of ranging.

4.4 Discussion and Conclusion

4.4.1 Home range utilization

Each orangutan included in the home range analysis exhibited stable home range behavior. Interestingly, there was substantial interindividual variation in the utilization of that home range. Larger home ranges typically translated to further average daily travel as evidenced by GAMM, however more travel did not translate to faster home range crossing times. Instead, home range crossing time was a function of how directed or how tortuous their overall space use was as measured by the velocity autocorrelation time scale. The standard deviation in tortuosity was 21.5 minutes, with no significant relationship to sex. Tortuosity was also not predicted by home range size. There are several possible factors that, upon future study, could explain the variation in tortuosity. Social behavior and variation in age may account for some variation in tortuosity. Perhaps young individuals searching for consortships may increase their likelihood of encountering conspecifics, or perhaps adult males are forced to modulate their motion in response to one another. Differences in locomotor strategy could possibly account for some tortuosity. Individuals constrained to the canopy may have markedly different movements than individuals locomoting on the ground, and there is evidence of a sex bias towards males having more prevalent ground-based travel (Ashbury et al, 2015). While this study did not collect this level of social behavior data, further thought is warranted on explaining the interindividual variation in tortuosity.

4.4.2 Male-female differences in space use

Collecting data on male orangutan ranging is famously difficult (Buckley, 2014). Attaching GPS collars is not possible due to the orangutan's throat sack. GPS data collection is therefore limited to using hand held GPS devices during focal animal follows. Furthermore, legal

restrictions on the ability to venture outside of study areas precludes following males when they leave site boundaries. Predicting when males will return to a study area is typically impossible. Few attempts at following males for prolonged periods of time have shown that male home ranges can be exceedingly large (e.g. Buckley, 2014). These constraints are true at Tuanan, resulting in very uneven sampling of males. For these reasons, all estimates of male home range size at Tuanan are likely underestimates due to sampling bias. Nevertheless, male utilization distributions at Tuanan are significantly larger than female utilization distributions. Males are also more likely to exhibit periodic patterns of space use within their home ranges.

Only two females exhibited periodicities in their mean location, with both females showing weak daily patterns of periodic space use. It is unclear why these two females are the only two exhibiting signs of daily periodic space use. They differ in both home-range size and age. Streisel is a young female with no offspring and a larger home-range, while Inul is a very old female that has had multiple offspring with a small home-range. No females showed evidence of monthly periodic behavior. All but one male showed evidence of periodic space use. There was substantial intermale variation in the time scale of the periodicities, with some males showing daily periods and others showing monthly periods. The intensity of the periodicities varied from as low as 15% variance explained to as high as 67% variance explained. There was no relationship to any movement parameters and the presence of periodicities. To the best of our knowledge, periodic space use in primates has not yet been studied, therefore ecological explanations for the presence of these periodicities are not yet obvious. There are a number of hypotheses that may explain some of this variation. Monthly periodicities could be explained by revisiting important renewable resources. If there is some food item that become available asynchronously, or renews on a monthly or lunar cycle, then monthly periodicities could indicate

both spatial and temporal knowledge of that resource. These periodicities may even indicate route-based search strategies or evidence of traplining and may aid future studies in examining how cognitive maps are encoded.

An alternative explanation for the presence of monthly periodicities may be social. Given the near complete home range overlap of the males at Tuanan, monthly periodicities may be the result of intermale competition. It is even possible that the cyclical space use of males is coinciding with female cycling, and that males return to areas in anticipation of mating opportunities with females. Future research could try to reconcile periodic behavior of males with long call data or resource renewal to try to contextualize the presence of these periodicities.

Majority of the orangutans exhibited a circulation process of around 1.5 months. This means that individuals are passing through the same parts of their home range on about a monthly cycle. Flanged males exhibiting both periodicities in their mean location and a circulation process are likely shifting to a different part of their home range at the end of each circulation, potentially looping through their home range as they deplete resources. High resolution remote sensing can aid in monitoring home range wide resource depletion in future studies.

Periodic patterns of orangutan space use seem to be a rich avenue of future research that will help us better understand the social and ecological drives of home range utilization.

4.4.3 Home range overlap

van Noordwijk et al., (2012) estimated female home ranges using traditional kernel density estimation and discussed female philopatry through the lens of home range overlap. AKDE utilization distributions indicate that the overlap of unrelated females was overestimated

by van Noordwick et al., (2012), and the overlap between related females was underestimated. Related females indeed exhibited a high degree of overlap between their utilization distributions, however GAMM revealed that within overlap zones there is substantial home range partitioning.

van Noordwijk et al., (2012) characterize related females as associating significantly more often than unrelated females and engaging in social behavior frequently during associations. While their association times are higher than that of unrelated females, the total percentage of days and percentage of time spent in association were remarkably low. van Noordwijk et al., (2012) report that the percent of days with encounters between related females is ~3 percent, and the percent of time in association during encounters is ~2 percent. We maintain that this is highly asocial and is in concordance with the degree of space use partitioning revealed by GAMM. This may be a spatial strategy whereby orangutans mitigate risk, tolerating a minimal level of resource competition provided individuals share a matriline.

The high degree of overlap between flanged male home ranges was unexpected. Orangutans have been classically portrayed as solitary, with a very loose and dispersed social structure in which there is only one resident flanged male (MacKinnon, 1974; Rijksen, 1978; Mitani, 1985, Galdikas, 1995). At Tuanan, it seems that several flanged males are range resident with nearly entirely overlapping ranges. Home range overlap amongst orangutans is thought to be higher at sites with higher population densities (Rijksen, 1978), and Tuanan has one of the highest known orangutan densities in Borneo (Husson et al., 2009). Anecdotally, there seems to be an impression amongst field researchers in Borneo that Tuanan and similar peat swamp sites are more productive, and able to support more orangutans than the dipterocarp dominated sites. Other more pessimistic field researchers seem to think the orangutan density at peat swamps is a function of habitat loss. In either case, Tuanan has a reputation for having a surprising flanged

male density, and males may be unable to avoid this degree of range overlap. Of the males included in this analysis, four of the seven have been observed at Tuanan since 2003/2004, with the others known since 2008 and 2012. These males not only overlap but have long overlapping tenures.

4.4.4 Travel distance between food patches

GAMM indicated that movement is more autocorrelated, and therefore more directed, when individuals are traveling distances beyond their perceptual range towards food resources. Long movements such as these are relatively infrequent, however when they occur they the movement is persistent. This mode of motion towards a resource not directly visible to the individual, suggests an intentional trajectory towards a location based on prior information. Janson and Byrne (2007) originally suggested motion beyond the perceptual range as the criterion for differentiating memory from taxis. Our results suggest orangutans may exhibit multiple modes of movement behavior, whereby they make frequent uncorrelated trips between detectable resources, with interspersed trips to known locations far away.

It is possible that relying on both local and non-local information is necessary for nutritional balancing. Orangutans may engage in short bouts of perceptual motion until they overshoot their macronutrient intake in protein or non-protein. They may then need to navigate towards a known resource that will return their cumulative nutrient intake to a target balance.

4.4.5 Nutritional mapping

The first step to modeling nutritional balancing was to recreate the nutritional landscape experience by the orangutans. The workflow involved rapid tree sampling through remote sensing, and tree identification through random forest.

Random forest prediction accuracy was between 70 and 83%. This level of predictive power is remarkable given the number of classes and the pixel-based approach implemented here. We would consider this level of error unacceptable for an empirical approach to modeling discrete choice, however since the approach here is to utilize simulation modeling, this level of accuracy is sufficient for approximating conditions at Tuanan. If 8 bands and ~2m resolution is enough to achieve >70% accuracy, then increasing the number of spectral bands and improving spatial resolution can improve model performance substantially. We plan to resample the site using drones, increasing the resolution to cm resolution. We also plan to increase the number of spectral bands when possible. Drone resolution data will be able to capture spectral variation at the level of fruit and leaves, and pick up subtle changes in height within tree crowns (Tang and Shao, 2015; Zhang, 2016). This can enable automated crown segmentation along with better prediction capabilities (Zagalikis et al., 2005; Smith et al., 2008; Seul et al., 2015). Improving our sampling to this extent will enable us to pursue an object-based classification approach, improving accuracy enough to pursue step selection and state space modeling.

4.4.6 Simulation

Simulation results suggest that perception-based strategies result in higher *Npe* consumption relative to memory-based strategies. One explanation for this could be that foraging

decisions are restricted to relatively local information, thereby causing individuals to be more susceptible to environmental stochasticity. This could in turn cause mean $Npe:P$ to be closer to the average of the environment, and therefore inflate proportional Npe intake. A strategy relying on prior, non-local information would enable individuals to buffer themselves from this by intentionally targeting resources not immediately available to them.

The perception model overestimated Npe intake when comparing model performance to observed values. The memory model performed surprisingly well, replicating the mean orangutan $Npe:P$ nearly exactly. This suggests that memory may be an important mechanism enabling orangutans to maintain their target ratio of $Npe:P$. The memory model assumed complete information about the entire habitat, an implausible expectation that we are not imposing on orangutans. Instead, orangutans are likely switching between modes of behavior where foraging decisions are based on resources within the perceptual range, then targeting known resources when local options can't facilitate nutritional balancing. This is evidenced by the high frequency of short, uncorrelated trips between resources, with rare long and autocorrelated trips present at the tail of the distribution of journey lengths (Figure 4.9).

The relationship between periodicities in space use and the evidence for a memory-based search strategy is an exciting topic for future research. Route based cognitive maps as well as temporal memory may result in periodicities in animal movement. Individuals could conceivably forage along a productive route, circling back at some characteristic timescale until nutritional balancing is no longer possible. They could then move to another set of foraging routes at some other known area within the home range, repeating this process. Clarifying the ecological context of periodic space use may enable us to address questions regarding cognitive maps and how information is encoded. Our simulation approach did not attempt to model how spatial memory

was encoded nor did it address temporal memory. Future studies may consider incorporating these elements into foraging models to better understand how they influence nutritional balancing.

While we simulated memory-based foraging on a nutritional landscape, it is important to note that individuals are not expected to be conscious of macronutrients as they forage. Individuals are most likely reacting to and remembering the food items themselves. Mechanistically, the spatial decisions behind macronutrient balancing are likely driven by something akin to cravings. An individual may satisfy its palate by feeding on a food rich in carbohydrates and lipids, causing it to reach an unbalanced macronutrient state, resulting in their subsequent craving to shift to an item rich in protein. There is some evidence that specific neuropeptides may control the intake of specific macronutrients, and that stimulating feeding and reward centers can cause molecular and neurochemical changes in the brain (Temple et al., 1998; Levine et al., 2003a; Levine et al. 2003b; Sharma et al., 2013). The degree to which neuropeptides affect macronutrient intake, and if they act on the same timescale as foraging decisions is an interesting avenue of future research. There is some literature on humans suggesting that the modern taste for non-protein energy evolved as a result of macronutrient availability in the past, whereby protein was highly available and non-protein was not (Speth and Spielmann, 1983; Cordain et al., 2000; Konner and Eaton, 2010; Kuipers et al., 2010; Raubenheimer et al., 2015). If this claim is supported, then it follows that orangutans may have had similar selection pressures resulting in their current target ratio of macronutrients. Neuropeptides may signal when to switch between food items, and memory-based navigation may have evolved to facilitate the acquisition of desired foods.

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Chapter 5. Conclusion

5.1 Summary and conclusions

Generations of researchers have contributed to our understanding of animal foraging and decision making. For years, the consensus has been that animals are essentially input-output bound. They have a limited amount of energy to allocate to behavior and are limited in their ability to intake energy (Schoener 1971; Krebs 1974). Therefore, they are thought to follow economic decisions rules regarding energy management (Pyke, 1984). As the foraging literature matured, researchers started asking more complicated questions, such as what do animals know and how do they use knowledge to make foraging decisions (Janson and Byrne, 2007). This line of questioning centered around animals' mental representations of space, since research acquisition is fundamental to energy optimization (Tolman, 1948; Pyke et al., 1977; Byrne, 1979; Bennett, 1996; Milton, 2000; Janson, 2000). Empirical attempts to address these questions were still locked into an energy in-energy out framework, and often struggled to find empirical support for spatial memory in foraging (reviewed in Janson and Byrne, 2007; Zuberbühler and Janmaat, 2010). We now know, however, that a plant is not just a plant (Freeland and Janzen, 1974; Glander, 1982; Cornell and Hawkins, 2003), and a calorie is not a just a calorie (Milton, 1979; Simpson and Raubenheimer, 1993; Felton et al., 2009; Raubenheimer et al., 2009).

Chapter two of this dissertation revisited our understanding of foraging goals, and explored whether nutrient balancing is a biologically relevant goal. Nutritional geometry metrics of foraging success (Simpson and Raubenheimer, 1995) were evaluated as against movement ecology metrics of directed behavior (Janson, 2000; Hill, 2006; Gurarie et al., 2009). First, simulation confirmed that the ratio of macronutrients consumed by orangutans could not be explained by chance. Then, examining variation in foraging success relative to variation in

spatial movement metrics revealed that orangutans modulate their spatial behavior in response to balancing macronutrients, and nutritional balancing was most successful when movement was goal oriented. This demonstrated that macronutrient balancing is a biologically meaningful goal influencing animal decision making, and definitions of foraging goals should be expanded to include nutritional balancing.

Chapter three utilized isoclines as a novel method for evaluating the quality of food items. Isoclines revealed that food items with seemingly disparate nutritional profiles may actually be equivalent from the perspective of orangutans. Nutritional profiles were then analyzed against preference indices (Lechowicz, 1982), showing that patterns of food preference are significantly related to balancing macronutrients. Demonstrating that the animal's own evaluation of resource value is linked to nutritional balancing gives further context and validation to the nutritional geometry framework. Additionally, the utility of isoclines for studying animal foraging is highlighted.

Chapter four implemented a continuous space continuous time approach to characterizing orangutan home range utilization (Calabrese et al., 2016). General patterns of space use, including male-female differences in home range behavior were discussed. Periodicities in orangutan space use were identified and discussed, and possible ecological contexts for said periodicities were explored. Movement between food trees by orangutans showed increased directedness during trips exceeding the orangutan perceptual range, suggesting utilization of prior information to navigate. The role of memory in nutritional balancing was explored via simulation modeling. Parameterization of movement models were informed by ctm estimated metrics. The model domain was generated using remotely sensed data and supervised machine learning techniques to recreate the nutritional landscape of Tuanan. Restricting foraging

decisions to the orangutans' perceptual range resulted in overestimation of non-protein energy intake. Prior information of the entire model domain resulted in a macronutrient balance nearly identical to observed orangutan intake. Results from chapter four suggest that spatial memory may be an important biological mechanism facilitating macronutrient balancing. It is likely that orangutans are able to prioritize protein because they have some prior information or prior experience enabling them to effectively navigate to resources with the desired ratio of macronutrients.

5.2 Future work

Future research is needed to clarify the ecological context of observed periodic patterns of orangutan space use. Periodic patterns of space use may provide clues into how information is encoded and may allow us to recognize signals of temporal memory. Understanding these relationships will enable future studies to model their effect on nutritional balancing.

Future improvements on nutritional mapping are necessary to take an empirical approach to studying memory and nutritional balancing. The methods used in this dissertation were appropriate for generating a simulation domain, however the prediction error and spatial resolution were not sufficient for an empirical approach. Utilizing drones and hyperspectral cameras would provide the resolution necessary to improve prediction accuracy, and to take an object based approach to tree classification (Zagalikis et al., 2005; Smith et al., 2008; Seul et al., 2015; Tang and Shao, 2015; Zhang, 2016). With a more reliable nutritional map, step selection functions can be utilized to empirically understand the drivers of orangutan travel routes, with the possibility of controlling for structural constraints on travel.

Finally, most work on nutrition and foraging, including this dissertation, have focused almost exclusively on macronutrient intake (i.e. Lee et al., 2002; Felton et al., 2009; Rothman et al., 2011; Martinez-Cordero et al., 2012; Simpson & Raubenheimer, 2012; Erlenbach et al., 2014; Solon-Beit et al., 2015; Felton et al., 2016). The human literature has recently made interesting advances on the role and importance of micronutrients to survival and health, identifying physiological and metabolic mechanisms that conserve micronutrient related processes (Ames, 2006; Hänsch and Mendel, 2009; McCann and Ames, 2009; Ames, 2010a; Ames, 2010b; McCann and Ames, 2011). If these mechanisms are important enough for triage mechanisms to have evolved, then micronutrient acquisition may be an important factor influencing decision making strategies. Currently, micronutrient work on non-human primates has been largely limited to the consequences of zinc and iron restriction on captive rhesus macaques, showing measurable differences in development and behavior (Golub et al., 2000; Golub et al., 2006a; Golub et al., 2006b; Golub et al., 2009; Golub, 2010; Golub and Hogrefe, 2014). Other notable studies include sodium acquisition by gorillas (Rothman et al, 2006), and copper intake by redtail monkeys (Rode et al., 2006). These studies open the door for examining the evolutionary implications of micronutrients on foraging behavior. Putting micronutrients in an ecological context, studying their relationship to macronutrients, and understanding their influence on the decision-making strategies is an exciting avenue for future research. Just as expanding our understanding of foraging goals has been a theme of this dissertation, perhaps future work will further expand how we define goals to include micronutrients.

5.3 Conclusion

In summary, the work culminating from this dissertation provides compelling evidence that orangutan spatial decisions are related to macronutrient balancing, and that prior information is utilized to achieve this. The nature of foraging goals is clearly more nuanced than previously assumed, and an individual's evaluation of a goal can change depending on immediate physiological demands. Proportional macronutrient intake should not be dismissed as phenomenological noise, and should be considered in studies of cognition and space use.

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